

THE ROLE OF RESOURCE AVAILABILITY AND HABITAT QUALITY IN
STRUCTURING PRAIRIE BEE COMMUNITIES

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THE ROLE OF RESOURCE AVAILABILITY AND HABITAT QUALITY IN STRUCTURING PRAIRIE BEE COMMUNITIES

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Wild bees are a rich natural resource. They help maintain ecological structure and function through pollination services, which promote gene flow among plant communities. As prairie landscapes are converted to cropland, the distribution of forage and the nesting resources that sustain viable bee populations changes. Furthermore, resource availability differs by species' natural history traits, and few studies examine bees' trait-based responses to changes in resource distribution across landscapes. In this dissertation, I examine how prairie bee assemblages, and their functional composition, are structured by floral resource availability, habitat quality, connectivity, and landscape composition. Results suggest that well-connected grasslands may currently serve as reservoirs of diverse suites of wild bees and robust pollination services, but they may be restricted to this landscape. Blooming forb abundance and diversity were the best predictors of bee abundance and diversity, respectively. Woodland cover was a stronger predictor of social species' abundances than solitary, as well as of wood- and cavity-nesting species than ground-nesting species. Habitat connectivity, particularly the betweenness centrality of a foraging site, was an important predictor of solitary bee abundance, whereas flux, the ability to disperse to or from a forage patch, was a better measure for social species. Bee distributions were mapped across the landscape as a proxy of pollination services, and those provided by social species were the most

continuous. However, services decline when landscape composition exceeds 17% crop cover or has less than 37% grassland cover. These are important thresholds for bee conservation strategies. Overall, results indicate that high-quality, well-connected landscapes, in their current condition, may serve as an oasis for wild bees, where pollination still functions at a high level in an otherwise highly fragmented ecosystem.

DEDICATION

For Grandma

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CHAPTER 1: INTRODUCTION

Native bees are a rich natural resource. Through pollination, they are tightly linked to the plant communities of terrestrial ecosystems and have a critical role in the maintenance of species and genetic diversity (Albrecht et al. 2012). In turn, this diversity contributes to resilience, an essential attribute of natural communities facing habitat loss, fragmentation and anthropogenic change (Elmqvist et al. 2003; Fischer et al. 2006).

The association of biodiversity and ecological functioning is often positive (Schwartz et al. 2000; Srivastava and Vellend 2005; Blvanera et al. 2006) and higher diversity is needed to sustain multifunctionality (i.e. several ecological functions operating simultaneously) within ecosystems (Zavaleta et al. 2010). Pollination function has been positively correlated to the abundance and species richness of pollinators (Kremen et al. 2002; Klein et al. 2008; Slagle and Hendrix 2009) but as research in pollination ecology has increased, declines in many pollinating organisms, particularly the abundance and diversity of bees, have been increasingly reported over the past few decades (Biesmeijer et al. 2006, Winfree et al. 2009). Declines are primarily attributed to the loss, fragmentation, and degradation of natural habitats (Brown and Paxton 2009; Keitt 2009; Winfree et al. 2009) since this reduces the availability of the nesting and forage resources required for successful reproduction and the persistence of pollinator populations (Westrich 1996; Kremen et al. 2004).

Grasslands are among the most highly fragmented ecosystems in the world. Tallgrass prairie, in particular, is a globally endangered ecosystem (Ricketts et al. 1999), consisting of rich and highly productive plant communities. Less than 1% remains of the

historic extent of tallgrass prairie in the Great Plains of the United States, and only about 2% of Nebraska's former tallgrass prairie remains; this is as small, highly fragmented patches (NGPC 2005). Loss via gradual conversion to agriculture (Samson et al. 2004) has had negative impacts on the flora and fauna of prairie ecosystems (Samson and Knopf 1994). The persistence of remaining fragments largely depends on maintaining and restoring ecological connections between species (Travers et al. 2011). Plant-pollinator relationships are especially important since functional diversity in the pollinator community enhances pollination efficiency, genetic diversity, and gene dispersal throughout the plant community (Travers et al. 2011). In this way, plant-pollinator interactions have an essential role in structuring terrestrial ecosystems (Steffan-Dewenter et al. 2006).

Numerous studies have investigated prairie bee communities and their temporal variability in the Great Plains region (e.g., Tepedino and Stanton 1981; Hines and Hendrix 2005; Davis et al. 2008; Kwaiser and Hendrix 2008). However, documenting and monitoring diversity within threatened habitats remains a conservation priority. A recent review which covered more than a century of forest and prairie plant-pollinator interaction data from the eastern edge of the former tallgrass prairie region identified network changes due to asynchronous shifts in forb and bee phenologies which, in turn, have caused disruptions or loss of temporal and spatial co-occurrence of extant species, as well as nonrandom species extinctions as landscapes became modified by agriculture (Burkle et al. 2013). Certain bumble bee species, for example, have experienced extreme reduction in genetic diversity, accompanied by population declines as high as 96% (Cameron et al. 2011). Although it is encouraging that many plant-pollinator interaction

networks exhibit a high degree of flexibility despite these phenological shifts and bee species extinctions, redundancy within network structure, the strength of interactions, and the very function of pollination have all declined (Burkle et al. 2013). Therefore, it remains important to continue to document species distributions in modified landscapes, to establish a baseline of the extant species assemblages of different types of grasslands and landscapes which have not yet been catalogued, and to monitor these assemblages to identify changes over time.

This project follows the systematic approach to conservation planning set by the Nebraska Natural Legacy Project (NGPC 2005) in a grassland pollinator context, one which targets wild bees specifically. This approach works to identify and prioritize those components of biodiversity (i.e. species assemblages, ecological communities, or habitats) upon which conservation efforts can focus to improve efficiency and effectiveness of strategies by increasing the likelihood of encompassing full suites of biodiversity (Margules and Pressey 2000; Groves 2003). This involves characterizing communities to establish baseline data, assessing the current status of species, and preparing for future monitoring. This is accompanied by exploration of drivers of species' distributions and abundances and it is useful to employ tools which help in identifying areas of potential concern on a broader scale. Importantly, because communities exist as components of a landscape mosaic, it is also valuable to examine them in the context of functional landscapes, in which the remnants of native communities are sufficiently intact for the ecological processes upon which the communities persist still function (Poiani et al. 2000). Some such landscapes have been

designated by the Nebraska Natural Legacy Project as Biologically Unique Landscapes (BULs).

Nebraska's prairie ecosystems can be categorized as tallgrass, mixed-grass, and shortgrass prairie. The tallgrass prairie ecoregion occupies the eastern quarter of the state. It abuts the sandhills to the north and the mixed-grass prairie to the west. The Southeast Prairies Biologically Unique Landscape was the primary study location for this research project and is located at the southeastern corner of the tallgrass prairie ecoregion in Richardson, Pawnee, Johnson, and Gage counties. Cropland is the dominant land use in the BUL but, in addition to generally more diversified farming practices in the tallgrass prairie ecoregion than in central and western ecoregions, there is a high concentration of native tallgrass prairie remnants (haymeadows and grazed pastures) within the BUL compared to the surrounding area (NGPC 2005).

Two secondary study locations were in the mixed-grass prairie ecoregion: one in the Central Platte River Biologically Unique Landscape in south-central Nebraska, which spans between Dawson and Hamilton Counties; the other in northern Holt County abutting the Lower Niobrara River Landscape and the Verdigre and Bazile Creek Watersheds Landscape. The mixed-grass prairie ecoregion is a transition zone between the tallgrass prairie to the east and the shortgrass prairie to the west where vegetation structure and composition vary with weather and topological conditions (NGPC 2005). Mixed-grass prairie species diversity is maximized by a combination of natural disturbances, including grazing regimes (Collins and Barber 1986). However, in this ecoregion of Nebraska, mechanized farming with center-pivot irrigation, fertilizers, and

pesticides has increased corn production, trending toward fewer and larger farms, and croplands now comprise two thirds of the area, leaving little remaining for grazing livestock (NGPC 2005).

The Natural Legacy Project has highlighted several common threats to grasslands within both ecoregions to which communities from each BUL are subjected. These include a general lack of awareness and knowledge of biological diversity, habitat loss via conversion to agriculture, and declining enrollment in the U.S. Department of Agriculture's (USDA) Conservation Reserve Program (CRP). Remaining grasslands and other ecosystems (woodlands and wetlands) are generally of high quality, although the importance of these fragments to biodiversity, and the complex ecological processes necessary to maintain them is poorly understood.

The broad goal of this research project was to characterize the wild bee communities of different types of grasslands in fragmented prairie ecosystems of Nebraska and assess the influence of local and landscape factors on bee diversity, species richness and abundance. Working with the hypothesis that local habitat quality and the amount of natural habitat in the surrounding landscape would have a positive influence on bee communities via the provision of floral and nesting resources, it was predicted that more diverse bee communities would be supported in habitats with greater floral resource availability and with greater proportions of natural habitat in the surrounding landscape. To better understand which characteristics most influence bee communities, a number of factors were measured, including local floral abundance and number of species in bloom,

habitat area, and the composition, configuration, and connectivity of suitable habitats within the surrounding landscape.

The specific research objectives were to 1) characterize and compare the wild bee communities of natural and semi-natural grassland habitats from three fragmented landscapes in eastern and central Nebraska, 2) determine the potential of floral resource availability to affect bee species assemblages, functional composition, and resource use within a subset of these habitats in the southeastern Nebraska landscape, 3) examine the potential for connectivity of suitable forage and nesting habitats within realistic foraging ranges of wild bees, as well as the composition and configuration of different land cover types to predict bee abundance and diversity, and 4) estimate wild bee abundance as a proxy of the level of pollination function across the entire Southeast Prairies landscape based on the resources offered by different land cover types for functionally different suites of wild bees. These objectives are divided among six chapters. After introducing the subject and providing context in the first chapter, the second chapter focuses on characterizing the bee assemblages from different habitat types in terms of species richness, diversity, and abundances. The third chapter examines the functional composition of wild bees within the Southeast Prairies BUL and the importance of floral resource availability for different suites of species according to functional traits and natural histories. The fourth chapter shifts focus to the different scales at which connectivity and resource availability across the landscape influence bees according to sociality, nesting strategy, floral specificity, and foraging capacity. The fifth chapter expands upon the distribution of resources beyond the focal study area and models the relative abundance of wild bees across the entire landscape of the Southeast Prairies

according to habitat suitability and species' attributes. Abundance indices are used as a proxy of the pollination services that are delivered within habitat patches by foraging bees. These indices can be used to identify areas where conservation efforts can be focused to maintain or enhance ecosystem functioning, as well as define area thresholds of relevant land cover types at which bees' services are expected to be limited. The sixth and final chapter is a discussion that summarizes and connects the main components of the research project. It describes how the project as a whole contributes to our understanding of how wild bee populations in Nebraska's prairie ecosystems are structured, and how future work can build upon these results.

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CHAPTER 2: THE COMPOSITION OF WILD BEE COMMUNITIES IN FRAGMENTED PRAIRIE LANDSCAPES

ABSTRACT

Bee diversity can be reflective of broader community biodiversity which is important for ecosystem stability. It can be a useful measurement in evaluating community response to conservation efforts as well as for identifying important structural differences in the assemblages of different natural and semi-natural grasslands which serve as reservoirs of pollinating species in modified landscapes. In this study I examined diversity and species composition of wild bee communities in natural and semi-natural grassland habitats from three locations in Nebraska. These included remnant tallgrass prairie, grazed pasture, and properties enrolled in the Conservation Reserve Program (CRP) within an agricultural landscape in southeastern Nebraska; adjacent remnant and restored prairie sites along the Platte River in central Nebraska; and high and low diversity CRP plantings within a single large CRP site in northeastern Nebraska near the Niobrara River. Comparisons were made within and between the three locations based on observed and estimated species richness, diversity estimates, and community similarity indices. Species compositions were compared with nonmetric multi-dimensional scaling and multiple response permutation procedures (MRPP), followed by indicator species analyses (ISA) to identify species with significant constancies within a location or habitat type. Although species dominance was high within all study locations and the similarity of species composition was low, few

differences were identified between the habitat types within each location. Species richness and diversity were greatest in the Southeast Prairies Biologically Unique Landscape, where a vulnerable bumble bee, *Bombus pensylvanicus*, was among the dominant species. Several oligolectic species were indicative of restored prairies in the Platte Prairies and halictids in the northern CRP site were dominant, especially over large species of Apidae, such as bumble bees. Taken together, the differences between the study locations suggest that environmental heterogeneity in the surrounding landscape, and the floral composition and successional age of restorations at the local level contribute to wild bee diversity in Nebraska prairies. Studies such as this not only document species compositions and provide baseline information on the distribution and status of wild bee species upon which future work can expand, but also provide insight to knowledge gaps that such work can address. Importantly, results justify current conservation efforts in these locations, encourage their expansion, and can be used to more specifically direct efforts to better support whole communities and entire suites of species.

INTRODUCTION

Biodiversity and ecological functioning are often positively correlated (Schwartz et al. 2000; Srivastava and Vellend 2005; Blvanera et al. 2006). This holds in the context of pollination function in that the level of pollination is positively correlated to the abundance and species richness of pollinating organisms (Kremen et al. 2002; Klein et al. 2008; Slagle and Hendrix 2009). This function is carried out predominantly by bees (Hymenoptera: Apoidea), and research in pollination ecology has increasingly reported declines in bee abundance and diversity over the past few decades (Biesmeijer et al. 2006, Winfree et al. 2009). This trend is primarily attributed to habitat loss, fragmentation, and degradation (Brown and Paxton 2009; Keitt 2009; Winfree et al. 2009) which reduces the nesting and forage resources required for sufficient reproduction for populations to persist (Westrich 1996; Klein et al. 2004).

Bee diversity can be a useful correlate for community biodiversity (Duelli and Obrist 1998; Tschamntke et al. 1998) and Richards et al. (2011) have proposed using it to measure community response to conservation efforts in grassland restorations. Natural and semi-natural grasslands are thought to serve as reservoirs of pollinating species (Öckinger and Smith 2007) and previous work has demonstrated the benefits of restorations to pollinators (Winfree 2010), particularly for enhancing species diversity and abundance (Fiedler et al. 2011; Williams 2011). Restorations that promote diversity are increasingly important for restoring plant-pollinator mutualisms, which in turn promote ecosystem stability (Winfree et al. 2008; Biesmeijer et al. 2010; Schweiger et al. 2010; Garibaldi et al. 2013).

Although not a true prairie restoration, in agriculturally intensive landscapes, the USDA's Conservation Reserve Program (CRP) is a type of habitat improvement where pollinator needs are more recently being considered. Pollinator planting mixes (such as CP42) are replacing cropland specifically for improving environmental quality. Harmon-Threatt and Hendrix (2015) note, however, that most "pollinator" seed mixes include species that more specifically benefit butterflies. They demonstrate that wild bee diversity could more closely reflect assemblages of remnant prairie preserves with the addition of just a few species which are highly attractive to bees. This not only highlights an area where conservation programs can be improved to promote wild bee diversity, but also the utility of natural habitats with which to compare communities in the evaluation of restoration practices for sustaining ecosystem functions.

This study was an examination of wild bee diversity within natural and semi-natural grasslands in the tallgrass and mixed-grass prairie communities of Nebraska. Remnant prairies, restored prairies, and CRP plantings were evaluated with three primary objectives: 1) document the species composition of three spatially distinct wild bee assemblages of Nebraska prairie, 2) assess the similarity of these communities, and 3) identify differences in the local composition of the wild bee assemblages between different natural or semi-natural habitat types within each location.

METHODS

Study locations and sites

This was an assessment of bee communities within and between three study locations in Nebraska (Figure 2.1; Appendices A-C), as a means of describing species

compositions and to determine differences in assemblages between different habitat types. The study was conducted from June to August in 2012, 2013, and 2014, with sampling occurring at least twice in each month, although the focal study location alternated between years. The primary study location was located in an agricultural landscape in southeast Nebraska, with specific study sites in Johnson, Pawnee, and Richardson Counties. All sites were located within an area designated by the Nebraska Natural Legacy Project as a Biologically Unique Landscape (BUL), this one being the Southeast Prairies BUL. A total of 15 sites were selected from three of the dominant grassland types in the area: remnant tallgrass prairie (also called haymeadow), grazed pasture, and properties enrolled in CRP. Five privately owned properties were selected for each grassland type based on management practices and landowner permission. The remnant prairies were managed for hay production, with haying occurring once per year. The grazed pastures were actively grazed by cattle during the study, although cattle were rotated between different pastures at different times. The CRP properties were all CP25 grass/forb seed mixes at least five years into their CRP contract. These natural and semi-natural grassland patches were sampled as representatives of different suitable bee habitat types within a mosaic of row crop agriculture (corn or soybeans), woodlands, and grasslands. These sites were sampled twice each in June, July, and August of 2012, and at least once in each of the same months in 2014 with the exception of two CRP sites that had been converted back to crop production after the first year and were therefore not available for sampling. Site size ranged from 7.6-58.4 acres.

The second study location was near the Platte River south of Wood River in Hall County, Nebraska. Study sites consisted of four remnant tallgrass prairie patches that

were each paired with a neighboring prairie restoration on property owned and managed by The Nature Conservancy. All sites were actively grazed by cattle and were paired in such a way as to keep environmental variables similar. The planting dates of restorations varied but all had been established for at least seven years. The sites were sampled twice each in June, July, and August of 2013.

The third and final study location was a large ($\sim 1.5 \text{ km}^2$) CRP site in Holt County near the Niobrara River in the northeast part of the State. The site was planted with two different seed mixes in 18 plots; these included nine with a low diversity mix (CP25, for rare and declining habitat), and nine with a high diversity pollinator mix (CP42, for pollinator habitat). The high diversity mix had been seeded in the fall of 2012, and spring of 2013, whereas the low diversity CP25 mix had been planted two years prior to study. Each plot within the site was sampled twice each in June, July and August of 2013 and 2014.

Bee sampling and identification

The wild bee assemblages were sampled with blue vane traps (SpringStar® Inc., Woodinville, WA, USA, Figure 2.2) suspended from a PVC pole at the level of the vegetation. Traps were set up for 48 hours during sunny conditions in the Southeast Prairies BUL, 24 hours in the Platte Prairies, and 24 hours in the Holt CRP plots. Four traps were distributed throughout each site in the Southeast Prairies, three traps were placed in each site in the Platte Prairies, and two traps were used in each plot of the Holt CRP site. In the Southeast Prairies and Platte Prairies, traps were placed such that they collected bees from across the whole site, which varied with the shape and size, and were

never fewer than 20 meters apart. In contrast, the Holt CRP plots were consistent in these features and therefore, traps were placed centrally and approximately 50 meters apart.

Upon retrieval, bees were transferred from the traps to Ziploc® freezer bags in the field, then placed in a freezer until specimens could be sorted and identified. Bees were identified to species when possible but some groups, such as *Lasioglossum*, were frequently identified only to genus or to morphospecies. *Agapostemon angelicus* (Cockerell, 1924) and *Agapostemon texanus* (Cresson, 1872) were considered the same species in this study since females cannot be distinguished based on morphological characters in populations west of the Mississippi River. Bees were first identified to genus using Michener et al.'s Bee Genera of North and Central America (1994) and Michener (2007), and then to species using a combination of keys on discoverlife.org, local keys to prairie bees of Missouri and a reference collection with confirmed species identifications that was created with professional assistance from Mike Arduser at the Missouri Department of Conservation, St. Louis Regional Office, St. Charles, MO, 63304 USA.

Species richness, diversity estimates, and dominance

Because communities consist of both common and rare species, which are unlikely to be equally represented with standard sampling techniques, it can be helpful to assess diversity by metrics which account for species' abundances in different ways, and to employ estimators that account for unseen species. Sampling sufficiency within each study location was assessed with sample-based rarefaction and extrapolation curves using the ecological statistics program iNEXT (Hsieh, Ma and Chao 2013). This curve plots

the species richness estimates for a rarefied sample based on the observed sample and an extrapolated sample up to double the observed sample size (Colwell et al. 2012).

Variance and 95% confidence intervals were computed with 100 replications of bootstrap resampling (Chao et al. 2013). Chao1 and an abundance-based coverage estimator (ACE) were used to estimate species richness. The former uses the number of singletons and doubletons to estimate the number of unobserved species and the latter, a non-parametric estimator, separates rare (fewer than 10 individuals) from abundant species and uses the rare group to estimate the number of unobserved species in the assemblage (Chao et al. 2003).

Diversity estimates based were computed in SPADE (Species Prediction and Diversity Estimation; Chao and Shen 2010) and EstimateS (Version 9; Colwell, 2012). Both Shannon entropy and Simpson index were considered because each gives different weight to dominant and rare species. Effective species estimates were calculated to provide a measure of the magnitude of differences between bee communities. Shannon entropy and its effective number of species (exponential of Shannon entropy) were computed using a jackknife procedure (Zahl 1977) and the Simpson index and its effective number of species (inverse of Simpson index) were maximum likelihood estimators (MLE; Magurran 1988, 2004). Schroeder and Jenkins (2018) are critical of the Simpson index because its favoritism of dominant species can be problematic with taxonomic or numerical undersampling, but they note its value in that it is independent of species richness and can therefore compliment other common diversity metrics.

Species dominance curves (i.e. rank abundance curves) were constructed to explore the nature of species distributions in the assemblage of each study location. The curves are formed by plotting the sum of observed individuals for each species against its rank in the assemblage and depict community structure in terms of the equitability of species abundances. In this case, species abundances represent the number of individuals observed per trap per sample day to keep abundances on the same scale between study locations.

Shared species and community similarity estimates

Community similarity between the study locations and habitats within them was measured with both incidence-based and abundance-based estimators to make comparisons with and without the influence of relative abundances. Multiple estimators were used to depict the potential range of similarity with different methods of calculation. The Sørensen similarity index is a qualitative measure of similarity on incidence data, whereas Bray-Curtis is a robust abundance-based index that use species-by-species comparisons of relative abundances between communities. A modified abundance-based Sørensen similarity index was also used as a means of accounting for the effects of undetected shared species (Chao et al. 2005). Finally, the Morisita index of similarity for three communities consists of two components: an overall measure based on the shared information between any two of the three communities (C23) and a global measure based on the proportion of individuals that are shared between all three communities (C33). Estimates of standard error were made with 200 bootstrap replications.

The similarities among the bee communities of the three study locations were visualized using nonmetric multi-dimensional scaling (NMS; Kruskal 1964; PC-ORD version 6, MjM Software, Glenden Beach, OR, USA). The ordination was based on relative Sørensen distances calculated from the proportional abundance of each species in the matrix, which emphasizes differences in the relative composition among communities rather than those that arise from the absolute abundances (McCune and Grace 2002). The ordination is based on ranked distances and is used to reflect patterns of covariation in response data. The final number of axes has no particular order of importance but represents the best mapping of species and site positions (Peck, 2010). Here, the best solution was determined through 250 runs on the relative Sørensen distance of species abundances per site within each study location.

Statistical Analyses

The significance of differences in bee communities observed with similarity indices and NMS ordination was tested with multi-response permutation procedures (MRPP; PC-ORD version 6, MjM Software), which compare differences among and between groups based on average within-group similarity. Here, the resulting p -value represents the probability of obtaining the observed average within-group distance (Peck, 2010). The Holm step-down procedure was used to correct for multiple comparisons. Because sampling effort was not equal between study locations, species abundances were converted to individuals per trap per sample day prior to analysis. The ordinations and MRPP tests were repeated after converting the data matrices to presence-absence data to assess whether the differences in communities were a consequence of species' identities

or relative abundances, since similar results with both data formats suggest the importance of species composition in explaining differences between sites and locations.

Several measures on the observed data were used to compare the bee communities between the different habitat types within each study location including species richness, relative abundance, Shannon entropy, evenness and effective species (the exponential of Shannon entropy). Evenness was included as a complement to Shannon entropy and species richness. It was measured as H/H_{\max} , where H is Shannon entropy and H_{\max} is its maximum value ($\ln[\text{species richness}]$). To account for species turnover with the progression of the season, data were converted to individuals per study site/plot per sample within three intervals of the flight season (early-, mid-, and late-season) which correspond to each of the three months in which trapping occurred. The significance of differences between CRP, grazed pasture, and remnant prairie in the Southeast Prairies BUL was assessed with a two-way repeated measures ANOVA using habitat type and flight interval as factors. Shapiro-Wilk normality tests and Brown-Forsythe equal variance tests were applied for all variables and the Holm-Sidak method was used for multiple comparisons. Community data for the Holt CRP study location failed Shapiro-Wilk normality tests for all variables except effective number of species in a two-way repeated measures ANOVA design and so a one-way repeated measures ANOVA with a combined factor of planting type (high or low diversity) and flight interval was used so that pairwise multiple comparisons of both factors could still be made. In this case, the Friedman repeated measures ANOVA on ranks and the Tukey test were used to determine significant effects of planting type within each flight interval. The remnant and restored prairie sites of the Platte Prairies study location were compared with a two-

way repeated measures ANOVA using the pairing of sites and flight interval as factors in a two-factor repetition design. Shapiro-Wilk normality tests and Brown-Forsythe equal variance tests were applied for all variables and the Holm-Sidak method was used for multiple comparisons. All ANOVA procedures were carried out in SigmaPlot 13.1 (Systat Software, San José, CA). Differences in species composition between habitat types at each study location were examined with separate multi-response permutation procedures (MRPP; PC-ORD version 6, MjM Software).

Finally, indicator species analysis (ISA; PC-ORD version 6, MjM Software) was used to determine which species were most responsible for the observed differences in bee community composition within and between study locations. This method is often used in conservation practices to link species to environmental conditions (Peck 2010), and it is useful here as a tool that measures the degree of species' constancies among grassland types.

RESULTS

A total of 109 species, 40 genera, and 5 families of wild bees were collected between 2012 and 2014 from the three study locations (Appendices D-F), over a quarter of which were represented by singletons (26.4%). The Southeast Prairies BUL was the largest and most extensively sampled study location, and 8,016 bees from 82 species, 33 genera and all 5 families were observed. This was followed by a near tie in terms of abundance between the Holt CRP site in northeastern Nebraska with 2,375 individuals, 34 species, 17 genera, and 4 families, and the Platte Prairies in south-central Nebraska with 2,297 individuals from 59 species, 26 genera, and 5 families. Of the 74.5% of the

overall bee species that were represented in the Southeast Prairies BUL, 40 were unique to that location. The Platte Prairies species composition covered 53.6% of the total species observed, 18 of which were unique to these sites. The Holt CRP location contributed 6 unique species and covered 30.9% of total observed species.

Within each location, most species were representatives of the families Apidae and Halictidae (Figure 2.3). *Melissodes* spp. were collected in the greatest numbers, with 22% of individuals in the Southeast Prairies, 57% in the Holt CRP, and 38% in the Platte Prairies. *Agapostemon* spp. followed in the Southeast Prairies and Holt CRP with 17% and 12%, respectively, but comprised only 5% in the Platte Prairies where instead, *Diadasia* spp. were more frequently encountered (27%). *Bombus* spp. were third most abundant in the Southeast Prairies (15%) and were followed by *Eucera* (11%), whereas *Eucera* and *Lasioglossum* spp. were next most common in the Holt CRP site (9.5% and 7%, respectively). In the Platte Prairies, *Lasioglossum* spp. comprised 8%, followed by *Agapostemon* spp. and *Bombus* spp., which were similarly abundant (4.4% and 4.6% of individuals, respectively).

Sample-based rarefaction and extrapolation curves suggest that each study location was well sampled, although the accumulated species on the Holt CRP curve was closer to reaching its asymptote than the Platte Prairies and Southeast Prairies (Figure 2.4). Likewise, the slope of the curve for the Platte Prairies at the point where extrapolation begins is steeper than that of the Southeast Prairies and may be further from its asymptote. Estimates of sample coverage (C) for each location were near complete, with all greater than 0.99 (Table 2.1), although further sampling may have reduced the

heterogeneity of samples within the Holt CRP and Platte Prairies sites where the coefficients of variation (CV) were greater than those of the Southeast Prairies BUL (Table 2.1; SEP: $CV = 2.04$; HLT: $CV = 3.03$; PLP: $CV = 2.98$).

COMMUNITY COMPOSITION BETWEEN STUDY LOCATIONS

Species richness, diversity estimates and dominance

Diversity estimates of different orders were in agreement with the observed numbers of species in terms of the ranking of study locations and the habitats within them (Table 2.1). Estimated species richness was greatest for the Southeast Prairies, with estimates as high as 100.3 ± 12.2 , followed by the Platte Prairies with 77.8 ± 13.1 and lastly was the Holt CRP with 38.1 ± 3.5 . The Chao1 estimators provided higher estimates than ACE for the Southeast Prairies and Platte Prairies but the ACE estimate was higher for the Holt CRP community. The difference between the observed and expected number of species for the Southeast Prairies was between 13-18 species, 17-18 species in the Platte Prairies, and 1-4 species in the Holt CRP site.

Estimated Shannon entropy followed the same pattern as estimated richness, with the greatest estimate given for the Southeast Prairies (3.106 ± 0.012), followed by the Platte Prairies (2.502 ± 0.033), and lastly Holt CRP (1.896 ± 0.031). Estimates of Simpson dominance showed highest dominance for the Holt CRP location (0.2988 ± 0.083) and the lowest for the Southeast Prairies (0.063 ± 0.011). The Holt CRP location's effective number of species was estimated at 3.347 ± 0.277 , compared to 5.998 ± 0.207 and 15.896 ± 0.178 for the Platte Prairies and Southeast Prairies, respectively.

Species dominance curves were constructed for the complete assemblage of bee species from the three locations combined (Figure 2.5a) as well as for each of the study locations individually (Figure 2.5b-c). The dominant species for the complete assemblage were *Agapostemon virescens* (Fabricius, 1775) and *Eucera hamata* (Bradley, 1942), followed by *Melissodes trinodis* (Robertson, 1901), *Melissodes comptoides* (Robertson, 1898), *Diadasia enavata* (Cresson, 1872), and *Bombus pensylvanicus* (DeGeer, 1773). All of these belong to the family Apidae except for *A. virescens*, which is in Halictidae.

The dominant species of the Southeast Prairies BUL were similar to those of the combined assemblage but *M. trinodis* had lesser dominance and *Xylocopa virginica* (Linnaeus, 1771) followed *B. pensylvanicus* (Figure 2.5b). *A. virescens* and *E. hamata* were followed distantly by *Agapostemon angelicus/texanus*, *M. trinodis*, and *M. comptoides* in the Holt CRP assemblage (Figure 2.5c). *M. trinodis* and *D. enavata* were dominant species in the Platte Prairies, followed distantly by *Melissodes agilis* (Cresson, 1878), *Anthophora walshii* (Cresson, 1869), and *B. pensylvanicus* (Figure 2.5d). All curves fall away steeply and have long tails of species with few or single individuals, indicating high dominance in all communities.

Shared species and community similarity

Of the 109 observed species, 21 were shared among all study locations (Table 2.2). The Southeast Prairies and the Platte Prairies shared the greatest number of species (38) and also had greatest estimates of similarity of for both incidence- and abundance-based estimators (classic Sørensen: 0.539 ± 0.018 , Bray-Curtis: 0.215 ± 0.006),

especially when the estimated number of undetected shared species was considered (abundance-based Sørensen: 0.903 ± 0.011). The Southeast Prairies and the Holt CRP locations had a similar number of shared species as that of the Holt CRP and Platte Prairies locations with 25 and 23 species, respectively, although in this case, the Holt CRP and Platte Prairies were more similar than the Southeast Prairies and the Holt CRP (Sørensen: 0.495 ± 0.026 vs. 0.431 ± 0.021 , Bray-Curtis: 0.171 ± 0.008 vs. 0.154 ± 0.005 , abundance-based Sørensen: 0.52 ± 0.014 vs. 0.48 ± 0.014). The three-community Morisita index (C33) shows a global similarity value much lower than the similarity when using information of any two of the three locations (C33: 0.031 ± 0.002 vs. C23: 0.132 ± 0.005), indicating that when species shared among all three communities are considered, the three locations are quite distinct.

The result of nonmetric multi-dimensional scaling of study sites and the wild bee species assemblage support the distinctness suggested by the three-community Morisita index (Figure 2.6). The solution to the ordination was a two-dimensional fit which explained 85% of the variation (52.5 and 32.5% for the two axes). The study sites were grouped by habitat type and clustered fairly neatly in “species space” according to study location. The Holt CRP site had the broadest range in the ordination but still had a clear grouping of the majority of this location’s study plots. The Southeast Prairies BUL was the most tightly grouped. The NMS on presence-absence data was qualitatively similar, explaining 84.9% of variation, although clustering was slightly weaker, particularly between the Platte Prairies and Southeast Prairies, and the ordination had a one-dimensional solution.

The results of the multiple-response permutation procedure on species compositions of all 109 species among the 41 sites and plots also supported the distinctness of study locations. The chance-corrected within-group agreement was $A = 0.3064$, $p = 0.0000$ and all pairwise comparisons of study locations were highly significant with p -values < 0.0001 even after Holm step-down procedure for multiple comparisons (Table 2.3). The MRPP on presence-absence data produced similar results, with the overall chance-corrected within-group agreement $A = 0.3412$, and the probability of getting a smaller or equal delta $p = 0.0000$, and all pairwise comparisons were again highly significant (Table 2.3).

Constancy was significantly greater for one study location over the others for several species (Table 2.4). Of the 20 species that were significantly constant to the Southeast Prairies, 13 (65%) were in the family Apidae, 5 (25%) were in Megachilidae, and 2 (10%) were in Halictidae. All *Anthophora* species except for *A. walshii* were significantly more abundant and constant in the Southeast Prairies than the other study locations. *Anthophora montana* (Cresson, 1869), *Coelioxys octodentata* (Say, 1824), *Dianthidium curvatum* (Smith, 1854), *Melissodes coloradensis* (Cresson, 1878), *Megachile fortis* (Cresson, 1872), *Triepeolus lunatus* (Say, 1824), *Xenoglossa kansensis* (Cockerell, 1905), and *Xylocopa virginica* were unique to the Southeast Prairies in this study. *X. virginica* was the only species with an indicator value of 100.0, or perfect indication, for any location since it was abundant and constant in all sites of the Southeast Prairies BUL but nowhere else.

Two species, *Agapostemon virescens* and *Eucera hamata*, had maximum indicator values in the Holt CRP location, but neither species was unique. The remaining eight indicator species were more abundant and constant to the Platte Prairies but none of these were unique to this location either. *Diadasia enavata* and *Melissodes agilis* had high indicator values (IV = 96.8 and 84.8, respectively) and although *D. enavata* was indicated as the most dominant species for this location in the rank abundance curves, *M. agilis* was distant third rank.

SIMILARITIES AMONG THE HABITATS WITHIN EACH STUDY LOCATION

Comparisons of the habitat types within the Southeast Prairies BUL

The similarity of different bee habitats within each study location was also assessed with shared species and incidence- and abundance-based estimators (Table 2.5). Among the three habitat types of the Southeast Prairies BUL, 46 species (56.1%) were shared by all, 56 (68.3%) were shared between CRP and remnant prairie, 50 (68.3%) were shared between CRP and grazed pasture, and 49 (59.8%) were shared between remnant prairie and grazed pasture. All estimates of community similarity were high, ranging from 0.814 ± 0.025 for the classic Sørensen index for CRP and remnant prairie to 0.999 ± 0.011 for the abundance-based Sørensen for the same habitats. Although the latter is the highest estimate of similarity given, all indices were higher and nearly identical for CRP vs. grazed pasture and remnant prairie vs. grazed pasture than for CRP vs. remnant prairie. The three-community Morisita index supports a high degree of similarity among all habitat types since the global similarity is only slightly lower than

that of the estimate of similarity for any two habitat types ($C33 = 0.943 \pm 0.023$, $C23 = 0.965 \pm 0.012$).

The high and low diversity plantings within the Holt CRP site shared 22 species (64.7%) and ranged in estimated similarity from 0.701 ± 0.019 for Bray-Curtis similarity to 0.974 ± 0.006 when the estimated number of undetected shared species is considered with the abundance-based Sørensen index. The remnant prairie and restored prairie sites of the Platte Prairies shared 37 species (62.7%) and similarity estimates fell within a similar range as the Holt CRP plantings, with 0.685 ± 0.015 for the Bray-Curtis estimate and 0.998 ± 0.008 for the abundance-based Sørensen index.

A total of 3,073 individual bees (38%) were collected from CRP habitats within the Southeast Prairies BUL. These represented 67 species from 29 genera, 7 of which were unique to this habitat type and represented by a single individual. *Anthophorula asteris* (Mitchell, 1963) was the only member of this genus to be collected and is unique among all the study locations. The most commonly collected species were *Melissodes comptoides* (328 individuals), *Eucera hamata* (326 individuals), and *Augochlorella aurata* (224 individuals).

A total of 2,054 individuals (26% of the Southeast Prairies total) were collected from grazed pasture and represented 58 species and 24 genera. Like the unique species of CRP, each of the six unique species found in grazed pasture were singletons. The only records of *Bombus fervidus* (Fabricus, 1798), *Megachile sculpturalis* (Smith, 1853), and *Xenoglossa strenua* (Cresson, 1878) in this study came from grazed pasture habitats in the Southeast Prairies. The most commonly encountered species were *Agapostemon*

virescens (269 individuals), *Melissodes comptooides* (193 individuals), and *Bombus pensylvanicus* (180 individuals).

The remaining 36% of bees collected from this study location were the 2,889 individuals, 64 species, and 26 genera from the remnant prairie sites. This habitat type contributed six unique species to the overall assemblage, three of which were singletons, and included *Ceratina calcarata* (Robertson, 1900), *Habropoda morrisoni* (Cresson, 1878), *Nomada affabilis* (Cresson, 1878), and *Nomia universitatis* (Cockerell, 1908). The most commonly collected species of remnant prairies were *Agapostemon virescens* (544 individuals), *Eucera hamata* (322 individuals), and *Bombus pensylvanicus* (251 individuals).

Few differences were identified in community similarity between habitat types in the Southeast Prairies (Figure 2.7) from multiple comparisons tests (Table 2.5). There were no significant differences for any community measures except for evenness ($F_{2,12} = 4.484$, $p = 0.035$) which was significantly higher in grazed pastures than remnant prairie habitats (Figure 2.7c; pasture mean: 0.785 ± 0.020 , prairie mean: 0.729 ± 0.012 , $p = 0.033$). Evenness was also significantly greater within pasture and prairie habitats in mid-season samples than early-season samples ($p = 0.040$ and $p = 0.014$, respectively). Species evenness among samples was significantly greater within prairie habitats for mid-season samples than late-season samples as well. Habitat type was not a significant factor for bee species richness or abundance in the Southeast Prairies BUL ($F_{2,12} = 2.545$, $p = 0.120$ and $F_{2,12} = 1.838$, $p = 0.201$, respectively) although species richness was significantly greater for early-season samples than late-season samples within CRP ($p =$

0.011) and prairie ($p = 0.039$) habitats. Abundance also differed significantly within CRP sites between early-season samples and mid- and late-season samples (E. vs. M.: $p = 0.036$; E. vs. L.: $p = 0.019$). Shannon entropy and Gini-Simpson values did not differ between habitat types ($F_{2,12} = 2.646$, $p = 0.112$ and $F_{2,12} = 2.349$, $p = 0.138$, respectively) but were significantly greater in mid-season samples from prairie habitats than late-season samples ($p = 0.004$ for both indices). Finally, the effective number of species was not significantly different among habitat types ($F_{2,12} = 2.752$, $p = 0.104$) although it was greater in mid-season samples within prairie habitats than late-season samples ($p = 0.012$).

The results of a multi-response permutation procedure performed on the community assemblage of the Southeast Prairies showed no significant differences in species composition between habitat types. The chance-corrected within-group agreement was $A = 0.0123$ ($p = 0.2872$). The difference between remnant prairie and CRP communities was approaching significance in pairwise comparisons ($A = 0.0428$, $p = 0.077$) but not after correcting for multiple comparisons ($p = 0.232$).

Comparisons of planting types within the Holt CRP study location

Within the Holt CRP location, 1,320 individuals (55.6%), 30 species, and 16 genera were collected from high diversity plantings compared to 1,055 individuals (44.4%), 26 species, and 13 genera from low diversity plantings. Of the 6 species unique to the location, three were unique to high diversity plantings, including *Agapostemon femoratus* (Crawford, 1901) and *Protandrena cockerelli* (Dunning, 1897). None were

specific to low diversity plantings. Mean species richness, abundance, community evenness, and Shannon entropy are plotted with standard errors in Figure 2.8 and each had considerable overlap of community measures between planting types. There was no significant treatment effect (planting type) on species richness (Table 2.6; $F_{8,5} = 0.487$, $p = 0.784$). Other variables failed Shapiro-Wilk normality tests and so the Friedman repeated measures ANOVA was used to test for effects of date and planting type using the combined factor of planting type within each flight period. A significant treatment effect was observed for bee abundance ($\chi^2(5) = 23.413$, $p < 0.001$) but the Tukey test revealed that this was due to a significant difference within the high diversity planting type between the mid- and late-season samples ($p = 0.001$). Both diversity indices were also influenced by the treatment ($\chi^2(5) = 16.879$, $p = 0.005$ and $\chi^2(5) = 24.076$, $p < 0.001$ for Shannon entropy and Gini-Simpson, respectively) but this was due to a significant difference between early- and late-season measures within the high diversity plantings and not to the effects of planting type. The equitability of bee communities was significantly greater in late-season samples than in either early- or mid-season samples ($\chi^2(5) = 27.389$, $p < 0.001$; L. vs. E: $p = 0.002$; L. vs. M: $p = 0.003$) within high diversity plantings. Effective species also differed significantly between treatments ($F_{8,5} = 0.766$, $p = 0.002$) but this was due to greater effective species (magnitude of differences in Shannon entropy between samples) within the high diversity plantings in early-season samples than late-season samples ($p = 0.005$). The MRPP performed on the species composition grouped by planting type showed no significant differences in the species assemblages within the Holt CRP site, meaning that within group agreement was not greater than between group agreement ($A = 0.00708$, $p = 0.2873$).

Comparison of remnants and restorations within the Platte Prairies

Most of the bees that were collected within the Platte Prairies study location came out of restoration sites, with a total of 1,400 individuals (61%) compared to 897 (39%) for the remnant prairie sites with which each was paired. A total of 52 species were observed in restoration sites from 23 genera. Twelve species were unique to this habitat type, 9 of which were singletons. Among these were *Epeolus* sp. and *Melitoma grisella* (Cockerell & Porter, 1899). These genera were collected nowhere else in this study. Fewer species were observed in remnant prairie sites, with 44 species from 22 genera, 4 of which were unique to this habitat type. These include *Perdita perpallidum* (Cockerell, 1901) and *Dieunomia triangulifera* (Vachal, 1897). *Dieunomia* spp. were only collected in these habitats during the study.

As was seen for habitat types within the Southeast Prairies BUL and the Holt CRP locations, there was little difference in community measures between the two habitat types of the Platte Prairies as measured by species richness, abundance, community evenness, and Shannon entropy (Figure 2.9). All measures are very similar and any differences in community measures in a two-way repeated measures ANOVA were negligible (Table 2.7). Species richness was varied only marginally between 19 and 32 species in remnant prairie sites (23.25 ± 5.97) and 20 and 38 species in restoration sites (27.00 ± 4.18) but was not significantly different between the two habitats ($F_{1,3} = 0.179$, $p = 0.701$), or within any flight period ($F_{2,6} = 0.340$, $p = 0.725$). Bee abundance was the most different of all community measures between remnant (224.3 ± 42.67) and restored (350.0 ± 107.7) sites, ranging from 114 to 321 in the former and 102 to 611 in the latter,

although this difference was not significant ($F_{1,3} = 1.323, p = 0.333$). The range of Shannon entropy for remnant sites was 1.339 to 2.897 (2.092 ± 0.356), which translates to 3.815 to 18.12 effective species, compared to 1.395 to 2.529 (2.048 ± 0.281) in restorations. When converted to effective species, the range of the latter is 4.035 to 12.541. Although the difference in the maximum effective species is fairly large, no significant difference was found between habitat types for either Shannon entropy or its exponential ($F_{1,3} = 0.536, p = 0.517$ and $F_{1,3} = 0.771, p = 0.445$, respectively). There was a significant interaction between habitat type and flight period for Shannon entropy ($F_{2,6} = 5.887, p = 0.038$), indicating that the effect of habitat type on this diversity index was dependent on the level of flight period, but multiple comparisons showed no significant difference between remnant and restored sites within any flight range of the sample season. There was also no difference between habitats for Simpson index ($F_{1,3} = 0.680, p = 0.470$) or community evenness ($F_{1,3} = 1.724, p = 0.281$). The range of latter was nearly identical, between 0.455 and 0.836 in remnant sites and between 0.458 and 0.844 in restorations. The MRPP on the species composition of the Platte Prairies site, grouped by habitat type, showed no greater similarity within each habitat than there was between them ($A = -0.10333, p = 0.9495$).

The indicator species analyses that followed MRPP tests revealed no species which were significantly abundant or constant to one habitat type over the other in the Platte Prairies and only a single species, *Agapostemon angelicus* (or *A. texanus*), that was significantly abundant and constant to one planting type (low diversity) over the other within the Holt CRP location (Table 2.8). In contrast, within the Southeast Prairies BUL

only grazed pasture habitats had no significantly abundant or constant species to achieve indicator status. A single species, *Lasioglossum nymphaearum* (Cockerell, 1916), with a maximum indicator value of 56.8, was significantly constant to remnant prairie habitats ($p = 0.0416$). Of the 8 species that were more abundant and constant in CRP habitats, *Apis mellifera* (Linnaeus, 1758) was closest to perfect indicator status, with an IV of 93.0 ($p = 0.0236$). None of the indicator species for CRP were unique to this habitat type, although *Melissodes coloradensis* was unique to the Southeast Prairies. It was also the only other indicator species, along with *X. virginica*, that was not present in at least two study locations. ISA was performed for each location separately to compare relative abundances in the context of equal sampling effort rather than converting the data to bees per trap per sample day to run the analysis on all seven habitats collectively, which would be less relevant to the relationships found in within-location analyses.

DISCUSSION

This study set out to describe the wild bee assemblages of Nebraska prairie from remnant and restored grasslands within three distinct locations. Observed and estimated species diversity measures were in general agreement in depicting the similarities and differences between the three study locations. Although species richness and diversity indices alone may be limited in describing community composition by masking patterns driven by relative abundances (Williams et al. 2001), this study employed multiple indices and included both species- and abundance-based estimates of richness and diversity to compare communities. Therefore, these results serve to complement other studies of bee communities in North American grasslands by incorporating relative

abundances into measures of community composition. With and without abundance data, however, the results of nonmetric multi-dimensional scaling and multiple response permutation procedures depicted three distinct communities, as suggested by the three-community Morisita index.

The Southeast Prairies Biologically Unique Landscape had the greatest species richness and diversity. This may be due primarily to it being the largest and most extensively sampled study location since positive species-area relationships are commonplace in ecology. Species richness is expected to increase as the size of quality habitats increases, but decrease with isolation from other habitats (Arrhenius 1921; Rosenzweig 1995), due to patterns of species extinctions and immigration (MacArthur and Wilson 1967). Similarly, landscape context may play a role since there was greater heterogeneity in habitats encountered throughout the sampled area in the Southeast Prairies than the Platte Prairies and Holt CRP locations. Habitat variety promotes diversity through distribution of resources (Ghazoul 2006; Yang et al. 2015). Additionally, since the three study locations were geographically distinct, landscape context, even if variable, may be entirely different in one location than another due to differences in environmental conditions across the eastern region of Nebraska. Central Nebraska is characterized by pivot irrigation row crops with isolated mixed grass and tallgrass prairie, the northern part of the region is sandhills and mixed grass prairie, and the southeast consists of large sections remnant tallgrass prairie and grazed pasture with comparatively little land area covered by pivot irrigation row crops, although row crops are still a dominant land use. This results in differences in the isolation and connectivity of habitat patches for each location amidst different matrices of natural habitats.

On a finer scale, site heterogeneity may also have contributed to greater species richness and diversity in the Southeast Prairies since three habitat types with different management practices were examined. Ecological niche theory considers the functional differences among species and the partitioning of the niches offered by environmental heterogeneity as driving patterns of species richness (MacArthur and Wilson 1967; Hortal et al. 2009). The Platte Prairies had less variable management, with cattle grazing practiced within both remnants and restorations as well as occasional controlled burns. In the Southeast Prairies, structural diversity of the plant communities of each habitat varied with three types of management: cattle grazing in pastures, haying in remnant prairie, and restriction of burning, haying, and grazing within CRP, leaving most of these sites with standing tall grasses. This variation in physical structure of vegetation at the local scale and resource availability at the landscape scale may explain the greater diversity of wild bees in the Southeast Prairies.

Community structure is typically characterized by abundances being unevenly distributed among species (Volkov et al. 2003), with a few species having the greatest abundance, and the majority being uncommon or rare. In this study, dominance was high within all locations, but the most abundant species varied between them. The Holt CRP site had the highest dominance (Simpson index = 0.299 ± 0.21), especially within high diversity plantings (0.388 ± 0.127), with *Agapostemon virescens* and *Eucera hamata* being the most abundant and constant to this location in indicator species analysis. *A. virescens* is a common, generalist, metallic sweat bee (Halictidae) with solitary to communal reproductive behaviors (Mitchell 1960). This species was dominant in blue vane traps in previous work as well (Stephen and Rao 2007). Previous studies have also

shown Halictid bees to prefer annual forbs, which are abundant in early successional stages dominated by weedy pioneering species (Steffan-Dewenter and Tscharntke 2001), and may partially explain the abundance of *A. virescens* within this study location. Other bees, including bumble bees and other Apidae, prefer perennial forb species which better satisfy the nectar needs of these larger species (Corbet et al. 1995), but which aren't well established until the second or third year of succession (Steffan-Dewenter and Tscharntke 2001). Taki et al. (2013) also found a lag in species richness and abundance for large social species in early successional stages of temperate forests compared to solitary bees and their cleptoparasites. It's worth noting that few bumble bees were collected from this location until mid- to late-season, and many fewer were collected the first season than the second.

E. hamata, a long-horn bee (Apidae), is a common, generalist species which is active in spring and early summer. Both *A. virescens* and *E. hamata* are ground-nesters. Within the high diversity plantings, there was a significantly greater number of bees collected in the early season. *E. hamata*, being a springtime bee, was responsible for this result since *A. virescens* is active throughout the season. The difference in bee abundance between seasons only in the high diversity plots may be the result of having been recently planted, leaving exposed soil in the spring and early summer since the plant community in these plots was not yet established. Soil-nesting species abundances have been shown to decrease as successional age increases (Steffan-Dewenter and Tscharntke 2001), and species composition will likely change over time, accompanying successional changes in the vegetation at this site. Other studies found, in contrast to general theory which predicts increasing species richness with increasing successional age, that bee species

richness peaked at the second year of succession in fallow fields and was associated with forb species richness at this stage while bee abundances were correlated to the area covered by forbs (Steffan-Dewenter and Tscharntke 2001; Kuussaari et al. 2011).

The Platte Prairies restorations are better established than the Holt CRP site, having been planted seven years or more before this study. The assemblage of this location had the second greatest dominance (Simpson index = 0.167 ± 0.035), but was more similar to the Southeast Prairies than the Holt CRP plantings. Species richness and diversity estimates predict greater abundance in the restorations of the Platte Prairies than remnant sites although no differences in species composition were detected. *Diadasia enavata* and *Melissodes trinodis* were dominant, but the two species indicative of the Platte Prairies over the Holt CRP and Southeast Prairies locations, *Anthophora walshii* and *Melissodes agilis*, followed distantly in the dominance curve. *A. walshii* and *M. agilis* are oligolectic species, specializing on pollen from partridge pea (*Chamaecrista fasciculata*; Mitchell 1962) and sunflower (*Helianthus* L.; LaBerge 1961), respectively. *D. enavata* also prefers sunflower but is known to visit other Asteraceae, such as thistles (*Cirsium* spp.; Linsley and MacSwain 1958). *M. trinodis* is a broader oligolectic within Asteraceae but sunflower is the primary pollen source (LaBerge 1961). The dominance and indicator status of oligolectes in the Platte Prairies may be a result, in part, of the types of plants selected for restoration. The benefits of restorations to the plant and pollinator communities are reciprocal, with pollinators responding positively in terms of diversity and abundance to the restoration of natural habitats (Fiedler et al. 2011; Williams 2011), and pollinator diversity contributing to the success and maintenance of the restoration by providing pollination services (Slagle and Hendrix 2009). Because of

declines in many native bees (Burkle et al. 2013), consideration of this dynamic is increasingly important for reconnecting plant-pollinator mutualisms (Menz et al. 2011), which, in turn, contribute to the stability of these ecosystems (Winfree et al. 2008; Potts et al. 2010; Garibaldi et al. 2013). Harmon-Threatt and Hendrix (2015) have demonstrated how restorations can promote wild bee diversity and abundance with the inclusion of just a few highly attractive forbs in restoration planting mixes. It may be especially important that selected species provide appropriate nutrition for development and reproduction (Vaudo et al. 2015).

The Southeast Prairies had the least dominance of the bee assemblages. The magnitude of the difference in diversity between the Southeast Prairies and the Platte Prairies was approximately 10 species, and nearly 13 species greater than the Holt CRP site. Like the Holt CRP site, however, *Agapostemon virescens* and *Eucera hamata* were the most abundant species. *Melissodes comptoides*, *Bombus pensylvanicus*, and *Xylocopa virginica* followed. *X. virginica* was unique to the Southeast Prairies and had an indicator value of 100.0. *Melissodes bimaculata*, *Anthophora montana*, and *Bombus bimaculatus* also had high indicator values for the Southeast Prairies but of these, only *M. bimaculata* was ranked among the most abundant in the dominance curve. *X. virginica*, the eastern carpenter bee, is a large wood-nesting species. It frequently nests in the wooden structures of rural development and fence posts (Arduser, *personal communication*). *M. comptoides* and *M. bimaculata* are common ground-nesting long-horn bees. Each is polylectic and active throughout the season. *A. montana*, like most of the Anthophorine bees, is a large ground-nesting bee although little information beyond taxonomy (Brooks 1983) is readily available.

Within the Southeast Prairies, the three-community Morisita index showed a high degree of similarity among all three habitat types in wild bee species composition, although CRP and grazed pasture were the most similar and CRP and remnant prairie the least. The equitability of species was greater in pasture than prairie, but no other differences were found between habitat types, either in diversity estimates or species composition. In grazed pasture, where species evenness was greatest, no species were sufficiently abundant or constant to achieve indicator status, whereas eight species were indicative of CRP and one species of prairie remnants. The latter was *Lasioglossum nymphaearum*, which has been considered an oligolege on aquatic flowering plants (*Nymphaea*, *Nelumbo*, and *Nuphar*) but has also been recorded on many other terrestrial forb species from multiple families (Mitchell 1960). The European honey bee, *Apis mellifera*, was a strong indicator of CRP (IV = 93.0) and may have been more abundant in these habitats because of the large amount of yellow and white sweet clover (*Melilotus officinalis* and *M. alba*) to which this introduced species is highly attracted (Ellis, *personal communication*). *Halictus ligatus*, another social species and a ground-nesting sweat bee, had the next highest indicator value (66.8), but was only approaching, albeit marginally, significantly greater abundance and constancy in CRP over grazed pasture and remnant prairie ($p = 0.052$). The four *Melissodes* species, *A. walshii* and *D. enavata* may all have been collected in greater numbers from CRP because of available nesting substrate, where bare ground was present at two large sites, or because of sunflower abundance within CRP sites. Several *Helianthus* spp. are often included in planting mixes for CP25 CRP in this part of Nebraska (Sprague *personal communication*). Additionally, CRP habitats may have had a greater number of indicator species because these sites offer

greater structural diversity in the vegetation, similar to the argument of site heterogeneity as a possible explanation of greater bee species richness and diversity in the Southeast Prairies over the other study locations. The structural diversity hypothesis proposes that low vegetation is less structurally diverse than tall vegetation (Morris 1971; Lawton 1983), and therefore provides fewer suitable niches for grassland insects (Southwood et al. 1979; Morris 2000). For example, moths and butterflies have demonstrated a preference for tall, successional grasslands over the short vegetation of grazed pastures in previous studies (Balmer and Erhardt 2000; Franzén and Ranius 2004).

Regardless of differences between habitat types within the Southeast Prairies, the abundance of bumble bees here may be especially useful in future conservation planning. *B. bimaculatus* is a common bumble bee but the Great Plains are on the western edge of its range (Williams et al. 2014) and so it occurs less frequently in Nebraska than the eastern United States. It is associated with wooded habitats and may have a co-evolutionary mutualism with woodland ephemerals (Colla and Dumesht 2010; Williams et al. 2014). *B. pensylvanicus* is listed as “vulnerable” on the IUCN Red List of Threatened Species and is nearly qualified for “endangered” status due to recent sharp declines in range, persistence, and relative abundance (Hatfield et al. 2015). Its dominance in the Southeast Prairies is encouraging as it may indicate sufficient high-quality habitat to sustain a reservoir of this and other pollinator species. Alternatively, its numbers here may indicate a shift in its range, perhaps as environmental conditions change. In a recent assessment of bumble bee distribution under modeled trajectories of peak greenhouse gas concentrations, Sirois-Delisle and Kerr (2018) found that of the 31 bumble bee species they considered, only *B. pensylvanicus* would be able to expand its range under all

climate change conditions given a realistic 10km/yr dispersal capacity. Furthermore, the overlap of expanding species' ranges was predicted to create certain "hotspots" for bumble bees in which conservation efforts may be focused (Sirois-Delisle and Kerr 2018). Without prior knowledge on the population of *B. pensylvanicus* in the Southeast Prairies, it isn't possible to claim it as evidence of such a hotspot, or that one is in the process of forming. Either scenario, however, presents opportunity to better understand species distributions in relation to resources, and to continue efforts to maintain the connectivity and quality of this landscape.

Conclusions

The wild bee assemblages of southeastern, south-central, and northeastern Nebraska grasslands were relatively distinct, sharing many common species but differing in those that were most dominant. Future research should obtain species composition data from additional locations within this ecoregion of Nebraska to detect species turnover along the gradient of change from tallgrass to mixed grass and sandhills. This may help to determine environmental conditions that account for differences in the larger wild bee community and possibly identify other areas where conservation efforts are needed to either maintain or restore diversity within the pollinator community. Although few differences were identified between habitat types at each location, the status of oligolectic species in restorations and the lag in the appearance of large social species in CRP plantings highlight the potential for carefully planned conservation efforts to influence the composition of the wild bee community through forb species selection and natural successional changes. Ensuring that the needs of wild bees specifically are

considered in planting mixes may promote both diversity and abundance of pollinators and the success of restoration efforts. However, there is currently little work that specifically evaluates mixes for bees (Winfree 2010), despite their status as dominant pollinators in most ecosystems (O'Toole and Raw 1991), and the ease with which planting mixes could be improved for bees with careful selection of highly attractive species (Harmon-Threatt and Hendrix 2015). Future research should work to this end, and importantly, apply improved management across landscapes since, as results in this study suggest, managing at the level of a plot or field alone may be inappropriate for conserving robust wild bee communities in modified landscapes. Finally, the status of a vulnerable species, *Bombus pensylvanicus*, with documented marked declines throughout most of its former range, among the dominant species of the Southeast Prairies wild bee assemblage may indicate that this landscape has potential to serve as a reservoir of pollinators and their services. Future research should investigate the distribution of this and other species throughout the ecoregion to delineate metapopulations and evaluate environmental conditions that contribute to persistence in the Southeast Prairies. Such knowledge would be valuable for making better informed conservation decisions that could restore the populations of these species on a larger scale, beyond the current boundaries of the Southeast Prairies.

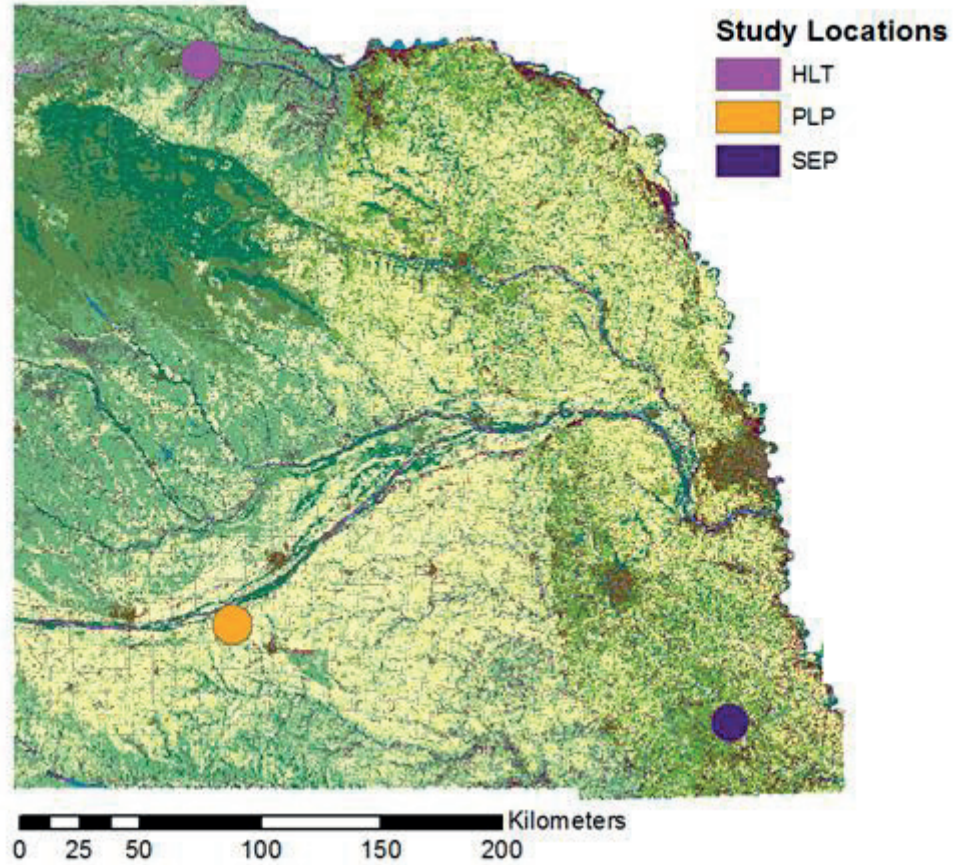


Figure 2.1. Three study locations in eastern Nebraska. The Holt CRP location (HLT) is represented by magenta and is just south of the Niobrara River in Holt County, Nebraska. The Platte Prairies location (PLP) is indicated with orange in south-central Nebraska, just south of Wood River in Hall County. The Southeast Prairies BUL (SEP) is indicated with dark purple and is located in the southeast corner of the state. Study sites were located in Johnson, Otoe, and Richardson Counties.



Figure 2.2. A blue vane trap. Depicted is an example of the trapping set up using a blue vane trap (SpringStar® Inc., Woodinville, WA, USA) hung from a PVC pole. The vanes are semi-transparent and reflective of ultraviolet light. The vanes are inserted into a funnel mechanism into which captured bees fall, and are then collected in the plastic jug. The shape of the funnel and jug prevent escape. Holes are drilled into the PVC pole every few inches so that the height of the trap can be adjusted to the height of the surrounding vegetation. Photo by Bethany Teeters, 2011.

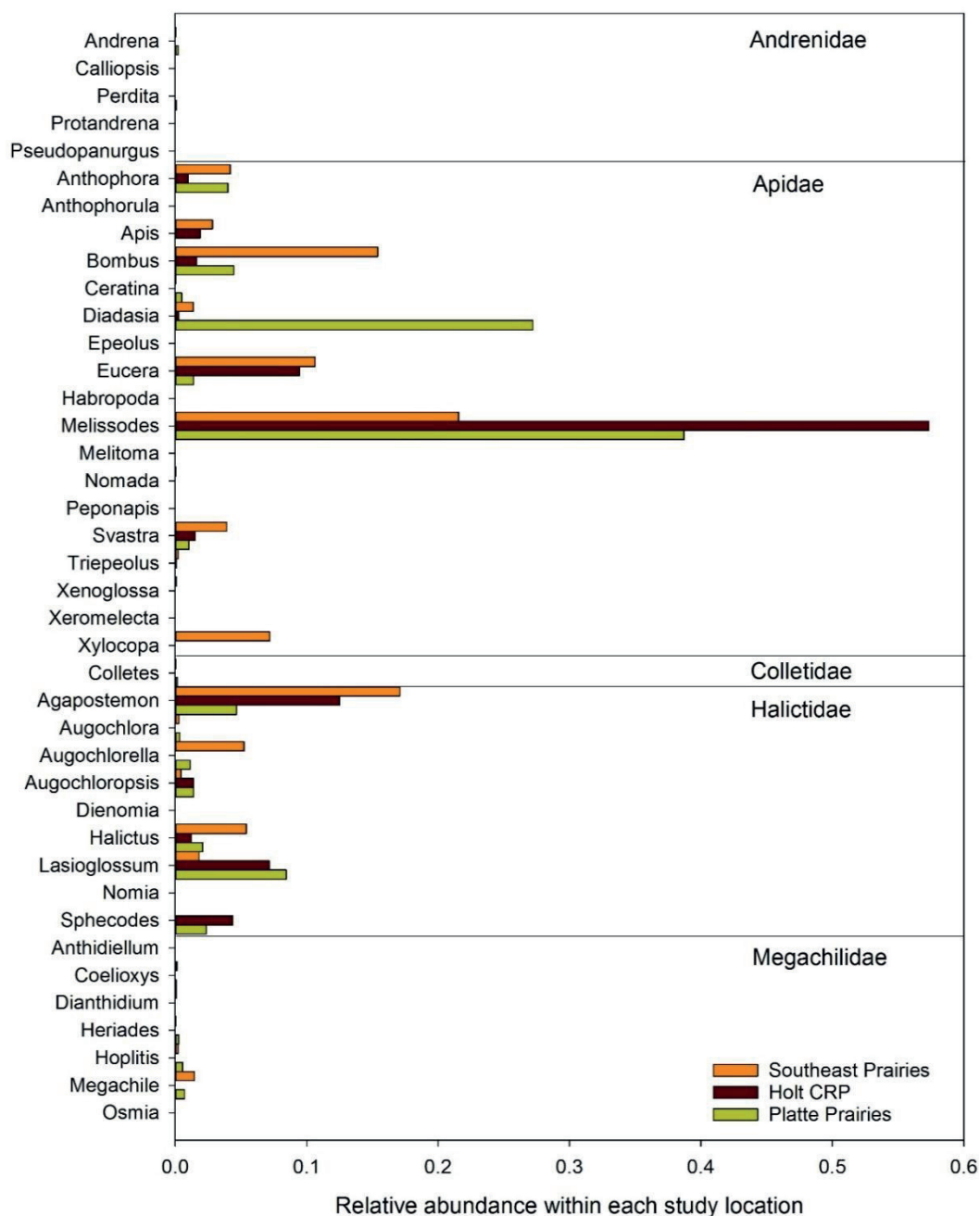


Figure 2.3. Distribution of wild bees among genera for each of three study locations. The relative abundances represent the proportion of individuals within each genus (listed by family) for the Southeast Prairies Biologically Unique landscape (orange), the Holt CRP site (maroon), and the Platte Prairies (green).

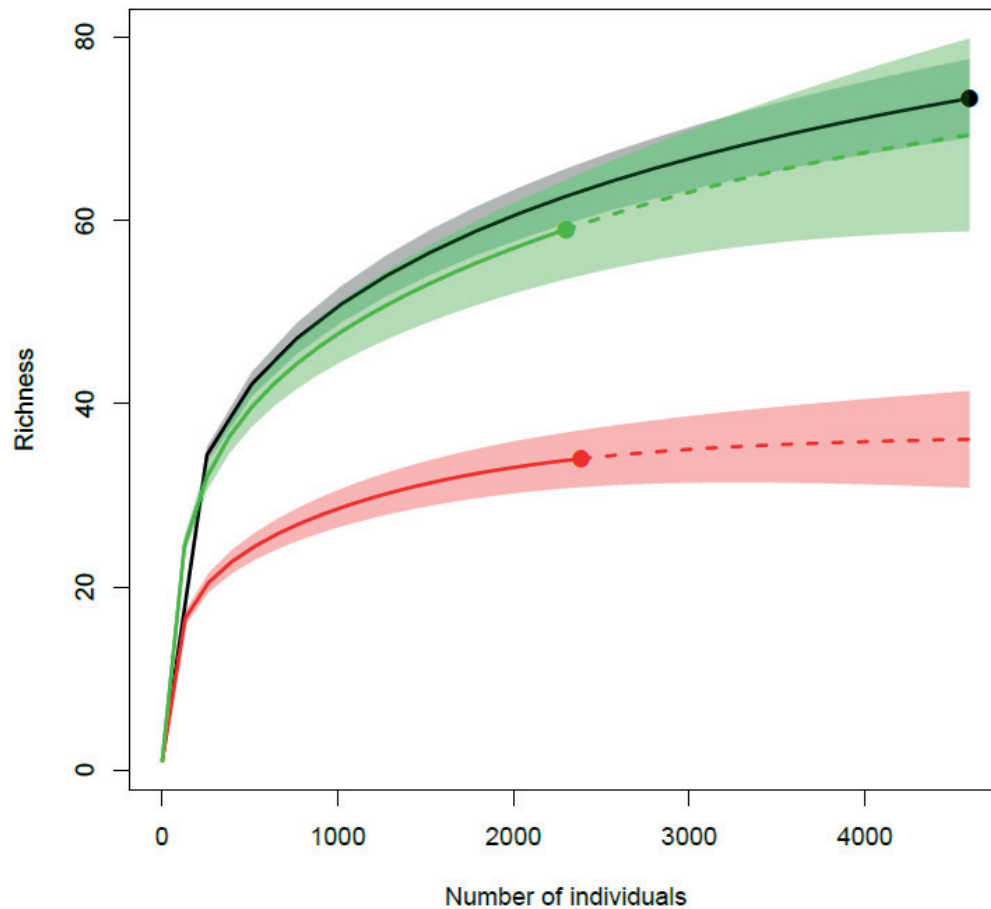


Figure 2.4. Sample-based rarefaction and extrapolation sampling curves for three study locations. Species richness estimates and 95% confidence intervals are plotted for a rarefied (smooth line) and extrapolated (dashed line) sample, with sample size up to double the size of the reference sample (solid dot). The Southeast Prairies BUL is indicated with black lines and confidence intervals. The Holt CRP location is represented by the red lines and confidence intervals. The Platte Prairies location is indicated with green.

Table 2.1. Observed species and estimated species richness, diversity, and effective number of species for wild bee assemblages from three study locations in Nebraska and the habitat or planting types within them. The number of observed species ($S_{(obs)}$), estimated richness (Chao1, ACE), diversity indices (\hat{H} , \hat{D}) and effective species ($\exp(\hat{H})$, $1/\hat{D}$) are listed. Estimated standard error is given in parentheses next to each estimate and confidence intervals are listed below it.

Location, Habitat & Coverage	$S_{(obs)}$	Species Richness (Chao1 & ACE)		Shannon Entropy & Exponential		Simpson Index & Inverse	
		Chao1	ACE	\hat{H}	$\exp(\hat{H})$	\hat{D}	$1/\hat{D}$
SE Prairies BUL	82	100.3 (12.2)	95.5 (7.1)	3.106 (0.012)	22.324 (0.318)	0.063 (0.011)	15.896 (0.178)
		CI: 87.6, 142.2	CI: 87.1, 117.7	CI: 3.081, 3.130	CI: 21.78, 22.86	CI: 0.041, 0.085	CI: 15.56, 16.24
CRP	67	92.6 (17.9)	83.3 (9.2)	3.189 (0.019)	24.257 (0.462)	0.057 (0.009)	17.65 (0.165)
		CI: 74.4, 155.2	CI: 72.8, 112.6	CI: 3.151, 3.226	CI: 23.35, 25.16	CI: 0.039, 0.075	CI: 17.23, 17.87
Pasture	58	72.0 (9.9)	72.1 (8.0)	2.994 (0.025)	19.964 (0.493)	0.070 (0.013)	14.298 (0.184)
		CI: 62.0, 106.8	CI: 63.0, 97.6	CI: 2.95, 3.042	CI: 19.0, 20.93	CI: 0.045, 0.096	CI: 13.85, 14.57
Prairie	64	89.6 (17.9)	80.2 (8.7)	2.910 (0.023)	18.355 (0.419)	0.084 (0.018)	11.903 (0.219)
		CI: 71.4, 152.2	CI: 70.1, 107.5	CI: 2.865, 2.955	CI: 17.53, 19.18	CI: 0.048, 0.120	CI: 11.43, 12.29
$C = 0.998, CV = 2.039$							
Platte Prairies	59	77.8 (13.1)	76.2 (9.3)	2.502 (0.033)	12.203 (0.401)	0.1667 (0.035)	5.998 (0.207)
		CI: 64.5, 123.4	CI: 65.4, 105.3	CI: 2.437, 2.566	CI: 11.42, 12.99	CI: 0.099, 0.234	CI: 5.59, 6.40

Table 2.1 (continued).

Location, Habitat & Coverage	Species Richness (Chao1 & ACE)		Shannon Entropy & Exponential		Simpson Index & Inverse		
	$S_{(obs)}$	Chao1	ACE	\hat{H}	$\exp(\hat{H})$	\hat{D}	$1/\hat{D}$
Remnant	44	74.3 (22.8) CI: 52.2, 156.4	62.5 (11.1) CI: 50.2, 98.9	2.689 (0.046) CI: 2.590, 2.78	14.719 (0.681) CI: 13.38, 16.05	0.1241 (0.024) CI: 0.077, 0.172	8.055 (0.195) CI: 7.67, 8.44
Restoration	52	84.0 (23.3) CI: 60.9, 167.0	70.8 (10.1) CI: 59.0, 102.5	2.327 (0.044) CI: 2.24, 2.414	10.251 (0.452) CI: 9.36, 11.14	0.202 (0.049) CI: 0.107, 0.298	4.946 (0.241) CI: 4.47, 5.412
$C = 0.993, CV = 2.980$							
Holt CRP	34	35.7 (2.2) CI: 34.2, 46.0	38.1 (3.5) CI: 34.9, 51.8	1.896 (0.031) CI: 1.835, 1.957	6.660 (0.208) CI: 6.252, 7.067	0.2988 (0.083) CI: 0.137, 0.461	3.347 (0.277) CI: 2.81, 3.89
Low	26	28.0 (2.6) CI: 26.3, 40.4	29.0 (3.1) CI: 26.6, 41.9	2.081 (0.041) CI: 2.002, 2.161	8.015 (0.326) CI: 7.38, 8.66	0.2170 (0.059) CI: 0.102, 0.332	4.607 (0.27) CI: 4.08, 5.14
High	30	43.5 (12.5) CI: 32.9, 92.9	42.0 (8.5) CI: 33.5, 71.6	1.646 (0.044) CI: 1.56, 1.732	5.187 (0.228) CI: 4.74, 5.634	0.3876 (0.127) CI: 0.138, 0.637	2.580 (0.329) CI: 1.936, 3.224
$C = 0.998, CV = 3.028$							

Notes: Estimated sample coverage (C) measures sampling completeness and the coefficient of variation (CV) estimates heterogeneity of species' detection probabilities. Chao1 estimates richness based on the number of singletons and doubletons (Chao, 1984). ACE (abundance-based coverage estimator) uses rare species ($n \leq 10$) to estimate unobserved species. Shannon entropy and its exponential are jackknife estimates (Zahl 1977) and Simpson concentration and its inverse are maximum likelihood estimators (MLE; Magurran 1988).

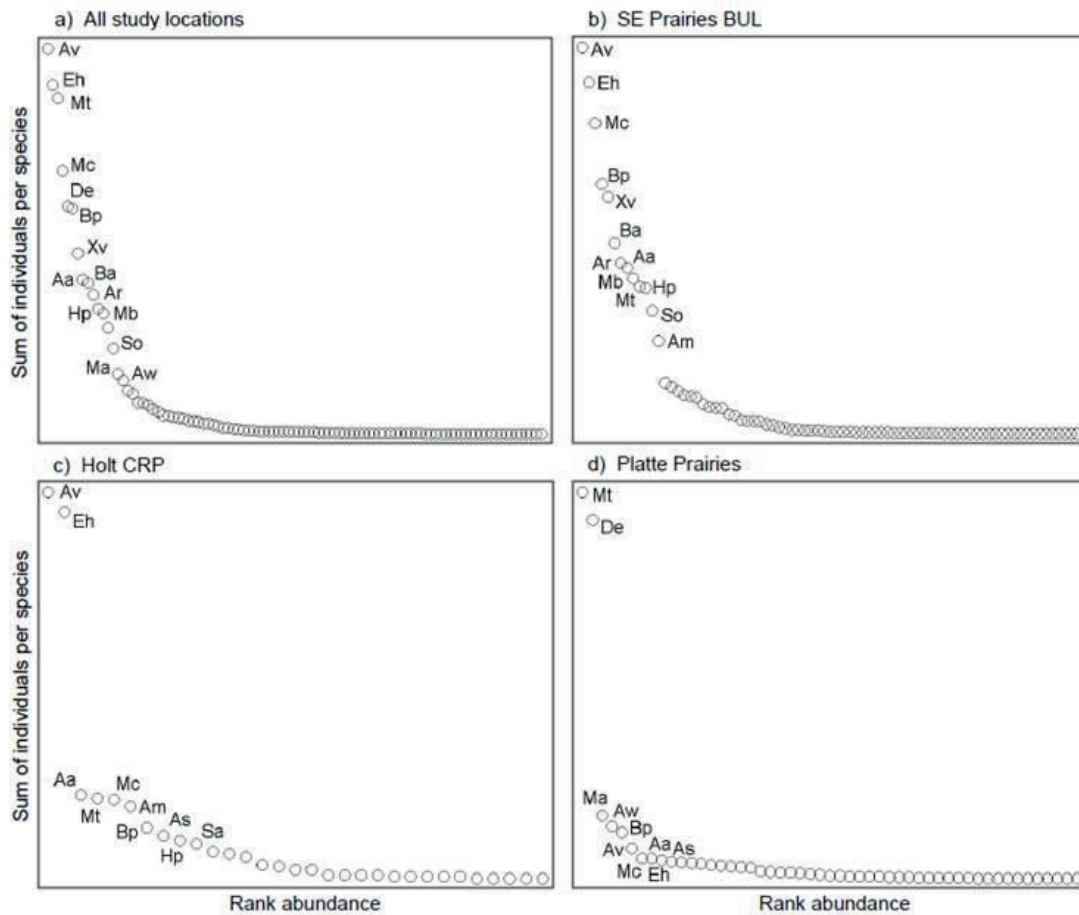


Figure 2.5. Rank abundance curves for wild bee assemblages showing a) the combined species assemblage from three study locations in Nebraska, b) the assemblage of the Southeast Prairies Biologically Unique Landscape, c) that of the Holt CRP location, and d) that of the Platte Prairies. Dominant species are labeled and represent the following: Aa—*Agapostemon angelicus/texanus*, Am—*Apis mellifera*, Ar—*Augochlorella aurata*, Av—*Agapostemon virescens*, Aw—*Anthophora walshii*, Ba—*Bombus auricomus*, Bp—*Bombus pensylvanicus*, De—*Diadasia enavata*, Eh—*Eucera hamata*, Hp—*Halictus parallelus*, Ma—*Melissodes agilis*, Mb—*Melissodes bimaculata*, Mc—*Melissodes comptoides*, Mt—*Melissodes trinodis*, Sa—*Svastra atripes*, So—*Svastra obliqua*, and Xv—*Xylocopa virginica*.

Table 2.2. Shared species and similarity of wild bee assemblages between and among the Southeast Prairies BUL, Holt CRP, and the Platte Prairies study locations. The number of shared species (S_{sp}) and similarity indices are given for the Southeast Prairies BUL (SEP), Holt CRP (HLT) and Platte Prairies (PLP). Estimated standard error is given in parentheses.

Assemblage Pairs	Incidence-Based Similarity		Abundance-Based Similarity		
	S_{sp}	Sørensen (classic)	Bray-Curtis	Morisita-Horn	Chao-Sørensen
SEP—HLT	25	0.431 (0.021)	0.154 (0.005)	0.156 (0.01)	0.480 (0.015)
SEP—PLP	38	0.539 (0.018)	0.215 (0.006)	0.248 (0.01)	0.903 (0.011)
HLT—PLP	23	0.495 (0.026)	0.171 (0.008)	0.057 (0.005)	0.520 (0.014)
Shared among all	21	Morisita similarity in 3 communities: C23-0.132 (0.005), C33-0.031 (0.002)			
					CI: 0.122, 0.142 CI: 0.027, 0.035

Notes: Sørensen (classic) is a qualitative index for incidence data. Chao-Sørensen is a quantitative estimator corrected for unseen species (Chao et al. 2005). Bray-Curtis is an uncorrected quantitative Sørensen similarity index. The Morisita-Horn index is a maximum likelihood estimator (MLE) that uses proportion data (Magurran 1988, 2004). Three-community Morisita similarity has two components: C23—similarity based on information in any two communities; C33—global similarity considering shared species of all 3 communities (Jost 2008).

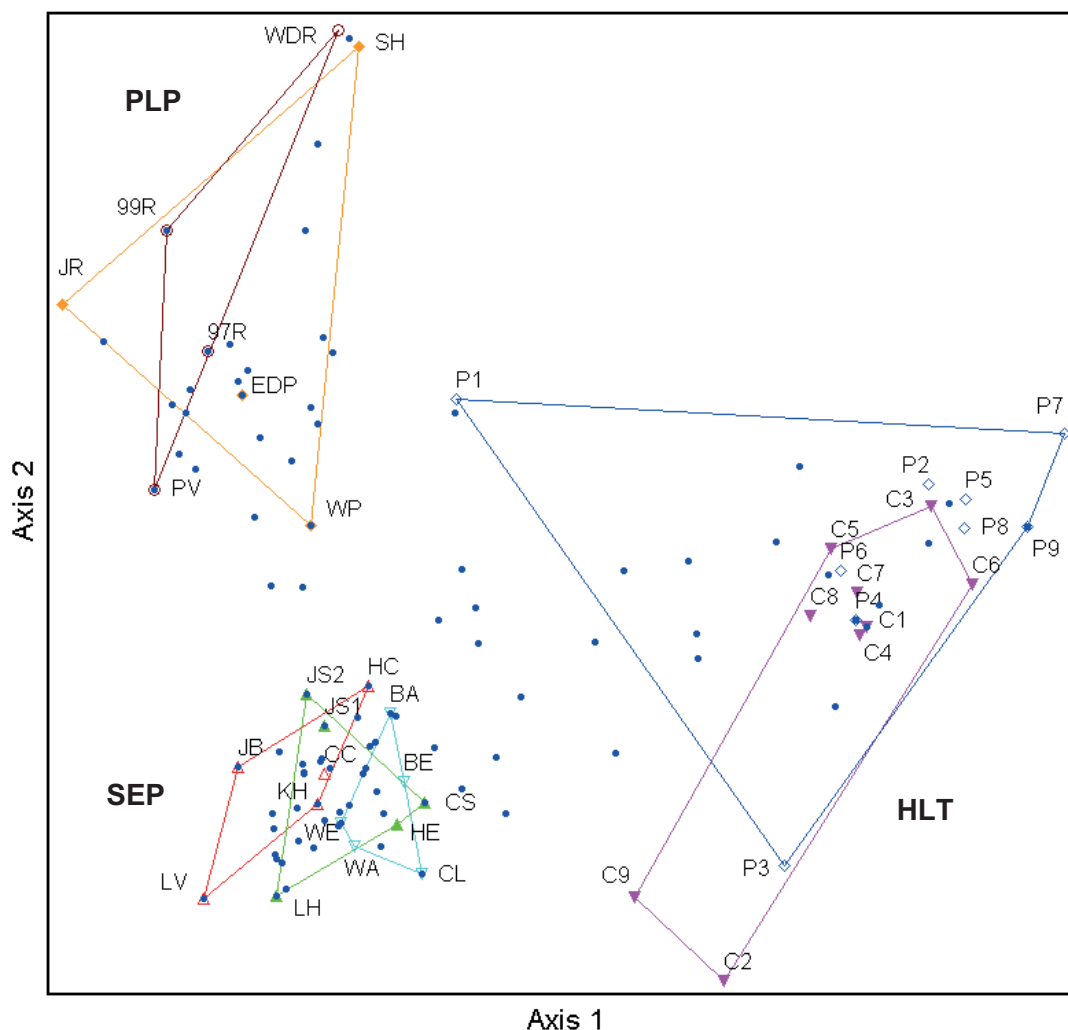


Figure 2.6. Nonmetric multidimensional scaling ordination of study sites overlaid on wild bee species assemblages for three study locations. Bee community ordination is a two-dimensional fit explaining 85% of the variation (52.5% for axis 1 and 32.5% for axis 2). Study sites are labeled with initials and the lines connecting them correspond to habitat or planting type. PLP represents the cluster of study sites for the Platte Prairies, HLT is the Holt CRP location, and SEP is the Southeast Prairies BUL. The blue points represent bee species.

Table 2.3. Indicator species analyses for wild bees from three study locations. Monte Carlo tests of significance on maximum indicator values (IV) are listed, as well as the mean IV, for the Southeast Prairies (SEP), Platte Prairies (PLP), and Holt CRP locations. Standard error is given in parentheses.

Bee species	Location (max)	IV	Mean (s.d.)	p-value
<i>Anthophora bomboidea</i>	SEP	65.3	27.8 (8.26)	0.0028
<i>Anthophora montana</i>	SEP	86.7	22.4 (8.11)	0.0002
<i>Anthophora occidentalis</i>	SEP	50.0	23.2 (8.84)	0.0154
<i>Augochlorella aurata</i>	SEP	67.1	30.2 (8.98)	0.0026
<i>Bombus auricomus</i>	SEP	77.4	28.3 (6.72)	0.0002
<i>Bombus bimaculata</i>	SEP	86.4	29.7 (9.52)	0.0002
<i>Bombus griseocollis</i>	SEP	52.7	25.3 (7.22)	0.0038
<i>Coelioxys octodentata</i>	SEP	33.3	12.8 (6.25)	0.0074
<i>Dianthidium curvatum</i>	SEP	26.7	11.0 (6.07)	0.0358
<i>Halictus parallelus</i>	SEP	47.6	35.7 (5.34)	0.0348
<i>Hoplitis pilosifrons</i>	SEP	35.4	17.7 (7.26)	0.0304
<i>Melissodes bimaculata</i>	SEP	88.3	25.5 (7.30)	0.0002
<i>Melissodes coloradensis</i>	SEP	66.7	17.9 (7.07)	0.0002
<i>Melissodes comptoides</i>	SEP	50.9	35.3 (8.07)	0.0470
<i>Megachile brevis</i>	SEP	80.2	23.1 (6.71)	0.0002
<i>Megachile fortis</i>	SEP	33.3	12.4 (6.32)	0.0086
<i>Svastra obliqua</i>	SEP	50.0	33.3 (6.05)	0.0142
<i>Triepeolus lunatus</i>	SEP	33.3	12.2 (6.11)	0.0074
<i>Xenoglossa kansensis</i>	SEP	26.7	11.2 (5.90)	0.0272
<i>Xylocopa virginica</i>	SEP	100.0	22.5 (6.95)	0.0002
<i>Agapostemon virescens</i>	HLT	56.2	42.5 (6.55)	0.0368
<i>Eucera hamata</i>	HLT	58.2	40.0 (5.80)	0.0078
<i>Agapostemon sericeus</i>	PLP	61.8	27.7 (8.56)	0.0028
<i>Anthophora walshii</i>	PLP	77.0	38.3 (7.97)	0.0002
<i>Diadasia enavata</i>	PLP	96.8	44.0 (12.13)	0.0002
<i>Halictus ligatus</i>	PLP	50.0	30.1 (9.29)	0.0362
<i>Melissodes agilis</i>	PLP	84.8	35.5 (7.88)	0.0002
<i>Melissodes communis</i>	PLP	47.3	16.4 (7.13)	0.0036
<i>Megachile montivaga</i>	PLP	47.6	29.2 (6.90)	0.0188

Notes: Location (max) indicates the study location in which the maximum indicator value (IV) was observed. The p -values listed represent the proportion of 4999 randomized trials in a Monte Carlo simulation in which indicator values equal or exceed the observed indicator value. A small p -value indicates that a species is more abundant and constant in a location than would be expected by chance.

Table 2.4. Shared species and similarity of wild bee assemblages from different grassland habitats within three study locations in Nebraska. The number of shared species (S_{sp}) and similarity indices are given for habitat types within the Southeast Prairies BUL (CRP, remnant prairie, and grazed pasture), Holt CRP (high and low diversity CRP plantings), and Platte Prairies (remnant prairie and prairie restoration). Both incidence- and abundance-based similarity indices are listed, including an abundance-based similarity measure for three communities. Estimated standard error is given in parentheses.

Assemblage Pair	Incidence-Based Similarity		Abundance-Based Similarity		
	S_{sp}	Sørensen (classic)	Bray-Curtis	Morisita-Horn	Sørensen (abundance)
Southeast Prairies BUL					
CRP—Prairie	56	0.842 (0.025)	0.814 (0.022)	0.945 (0.02)	0.999 (0.011)
CRP—Pasture	50	0.787 (0.027)	0.848 (0.02)	0.97 (0.016)	0.98 (0.013)
Prairie—Pasture	49	0.79 (0.023)	0.849 (0.022)	0.979 (0.016)	0.985 (0.012)
Shared among all	46	Morisita similarity in 3 communities: C23—0.965 (0.012), C33—0.943 (0.023)			
				CI: 0.942, 0.990	CI: 0.888, 0.991
Holt CRP					
High-Low	22	0.786 (0.036)	0.701 (0.019)	0.912 (0.016)	0.974 (0.006)
Platte Prairies					
Remnant-	37	0.771 (0.03)	0.685 (0.015)	0.936 (0.014)	0.998 (0.008)
Restoration					

Notes: Sørensen(classic) is a qualitative index for incidence data. Chao-Sørensen is a quantitative estimator corrected for unseen species (Chao et al. 2005). Bray-Curtis is an uncorrected quantitative Sørensen similarity index. The Morisita-Horn index is a maximum likelihood estimator (MLE) that uses proportion data (Magurran 1988, 2004). Three-community Morisita similarity has two components: C23—similarity based on information in any two communities; C33—global similarity considering shared species of all 3 communities (Jost 2008).

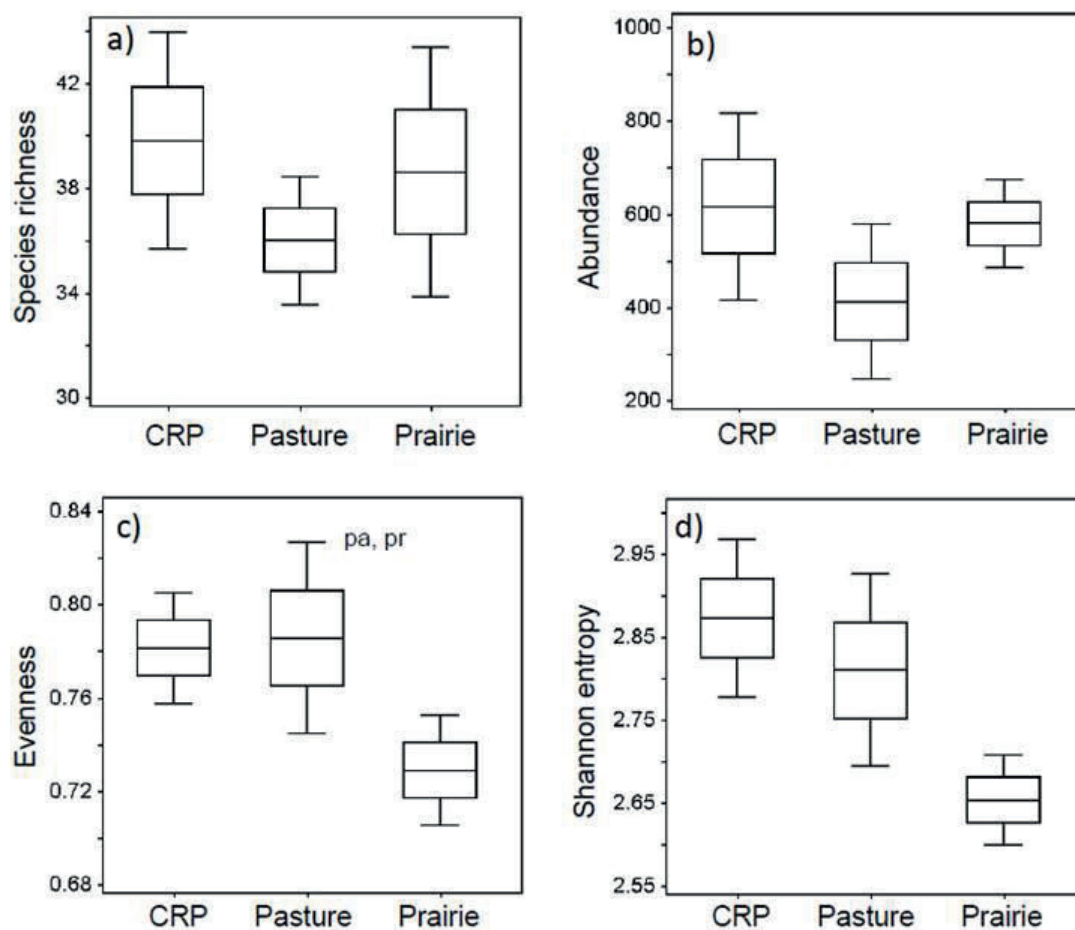


Figure 2.7. Comparison of a) species richness, b) abundance, c) community evenness, and d) Shannon entropy between three habitat types in the Southeast Prairies BUL. The means of each measure are plotted ± 1 s.e. Significant differences are noted with letters next to the greater box plot which indicate the habitats involved: cr for CRP, pa for grazed pasture, and pr for remnant prairie.

Table 2.5. Results of two-way repeated measures analysis of variance on wild bees collected with blue vane traps in three grassland habitat types of the Southeast Prairies Biologically Unique Landscape during early-, mid-, and late-season flight periods. Means are given for CRP (C), grazed pasture (G), and remnant prairie sites (R), ± 1 SE. The numbers listed from ANOVA represent *P* values. Bold face highlights significant factors. Significant contrasts are indicated by noting the components involved. Contrasts of site means were evaluated by the Holm-Sidak method of multiple comparisons with an overall significance level of 0.05.

ANOVA factor or Holm-Sidak contrast	Bee species richness	Bee species abundance	Shannon entropy (<i>H</i>)	Gini-Simpson index (<i>D'</i>)	Evenness (<i>H/H_{max}</i>)	Effective species (<i>expH</i>)
Mean	C: 39.80 \pm 4.604 G: 36.00 \pm 1.225 R: 38.60 \pm 2.379	C: 614.6 \pm 100.6 G: 410.8 \pm 83.24 R: 577.8 \pm 46.93	C: 2.872 \pm 0.106 G: 2.809 \pm 0.058 R: 2.653 \pm 0.027	C: 0.913 \pm 0.004 G: 0.911 \pm 0.007 R: 0.887 \pm 0.004	C: 0.781 \pm 0.027 G: 0.785 \pm 0.020 R: 0.729 \pm 0.012	C: 17.75 \pm 0.806 G: 16.71 \pm 0.929 R: 14.22 \pm 0.388
ANOVA results	df					
Habitat	2,12	0.120	0.112	0.138	0.035	0.104
Flight	2	<0.001	0.006	0.004	0.001	0.014
Habitat x Flight	4	0.624	0.303	0.471	0.690	0.361
Holm-Sidak contrasts						
1) Flight within CRP	(E vs. L)	(E vs. M, L)	no	no	no	no
2) Flight within Pasture	no	no	no	no	(E vs. M)	no
3) Flight within Prairie	(E vs. L)	no	(M vs. L)	(M vs. L)	(M vs. E, L)	(M vs. L)
4) Habitat within Flight	no	no	no	no	no	no

Notes: Site samples were pooled by capture month (June, July and August), and correspond to flight periods early- (E), mid- (M), and late-season (L) samples.

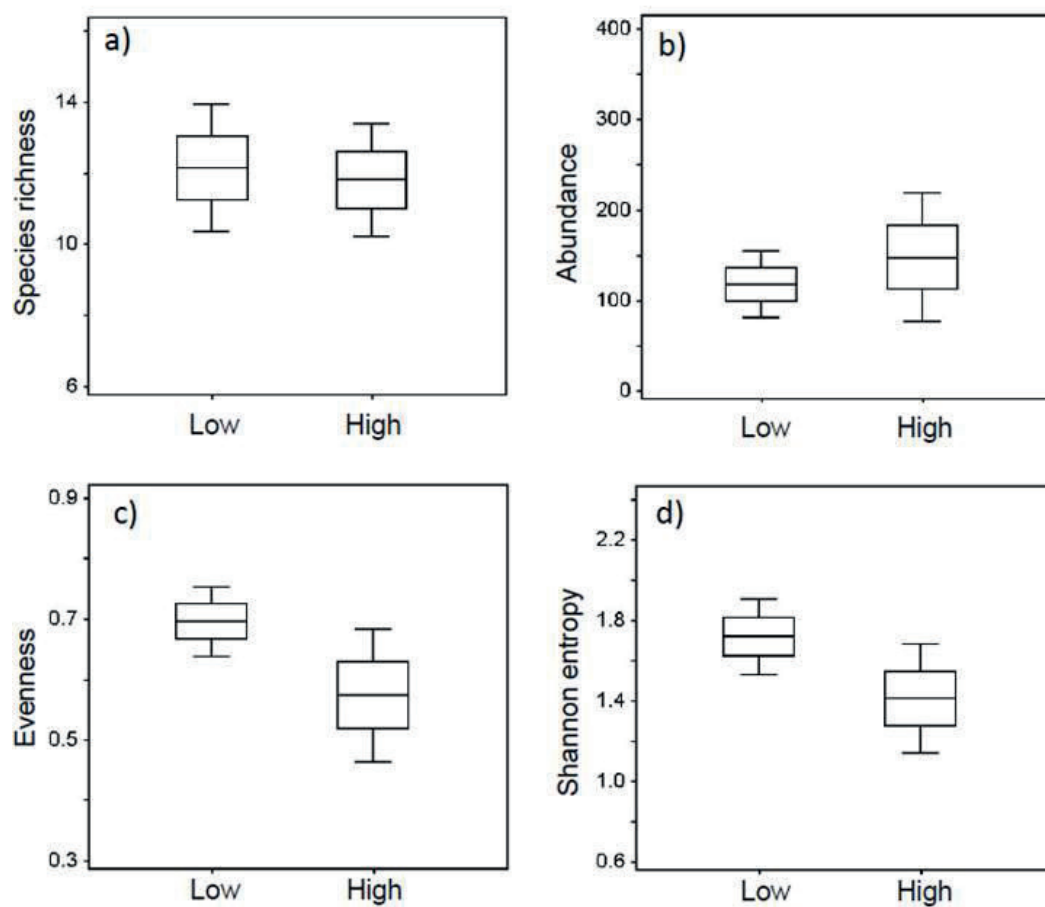


Figure 2.8. Comparison of a) species richness, b) abundance, c) community evenness, and d) Shannon entropy between low and high diversity plantings within the Holt CRP study location. The means of each measure are plotted ± 1 s.e. No differences were found between planting types and therefore, none are indicated in the plots.

Table 2.6. Results of one-way repeated measures analysis of variance and Friedman repeated measures analysis of variance on ranks for wild bee species richness, abundance, and diversity in high and low diversity plantings in the Holt CRP study location during early-, mid-, and late season flight periods. Means are given for high (H, CP42) and low (L, CP25) diversity plantings, ± 1 SE and P values are listed from ANOVA. Bold face highlights significant treatment effects at $P \leq 0.05$, which are indicated in comparisons by noting the components involved in the significant effect.

ANOVA factor, Holm-Sidak contrast, or Tukey Test	Bee species richness	Bee species abundance	Shannon entropy (H)	Gini-Simpson index (D)	Evenness (H/H_{\max})	Effective species (\exp^H)
Mean	H: 11.78 ± 0.795 L: 12.11 ± 0.889	H: 146.7 ± 35.45 L: 117.2 ± 18.57	H: 1.407 ± 0.136 L: 1.715 ± 0.094	H: 0.581 ± 0.059 L: 0.720 ± 0.028	H: 0.574 ± 0.055 L: 0.696 ± 0.029	H: 4.377 ± 0.545 L: 5.753 ± 0.540
ANOVA results	df					
Planting/Flight†	8,5	<0.001	0.005	<0.001	<0.001	0.002
Holm-Sidak or Tukey method‡						
1) Planting within Early	no	no	no	no	no	no
2) Planting within Mid	no	no	no	no	no	no
3) Planting within Late	no	no	no	no	no	no
4) Flight within High	no	(M vs. L)	(E vs. L)	(E vs. L)	(L vs. E, M)	(E vs. L)
5) Flight within Low	no	no	no	no	no	no

Notes: Planting type was combined into a single treatment factor with each of three flight periods: early- (E), mid- (M), and late-season (L), which correspond to capture month. Contrasts of site means were evaluated by the Holm-Sidak or Tukey method of multiple comparisons with an overall significance level of 0.05 for a standard one-way repeated measures ANOVA and a Friedman repeated measures ANOVA on ranks, respectively.

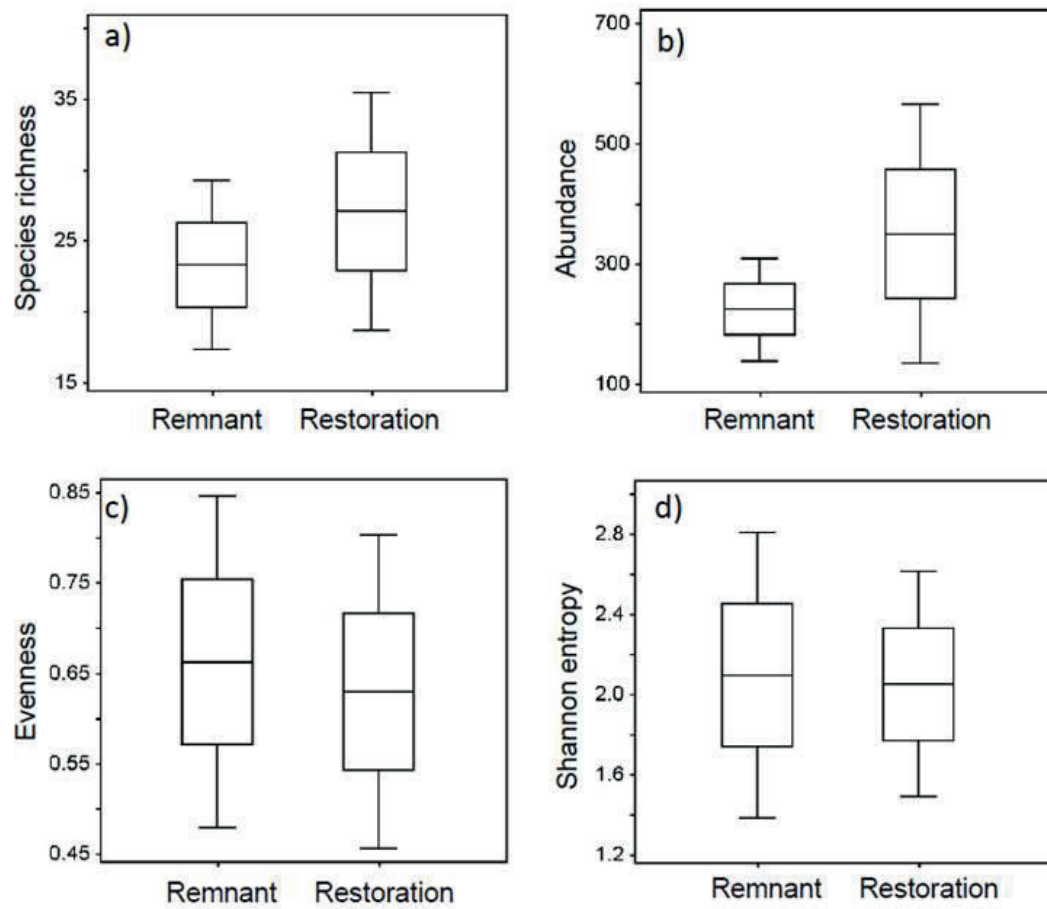


Figure 2.9. Comparison of a) species richness, b) abundance, c) community evenness, and d) Shannon entropy between remnant prairie and prairie restorations within the Platte Prairies study location. The means of each measure are plotted ± 1 s.e. No significant differences were found between remnants and restorations and therefore, none are indicated in the plots.

Table 2.7. Results of two-way repeated measures analysis of variance on wild bee species richness, abundance, and diversity in remnant prairies and restored prairies of the Platte Prairies study location during early-, mid-, and late season flight periods. Means are given for remnant (M) and restored (S) prairie sites, ± 1 SE and P values for ANOVA, with significant effects at $P \leq 0.05$ in bold and the components involved in the significant effect indicated for multiple comparisons.

ANOVA factor or Holm-Sidak contrast	Bee species richness	Bee species abundance	Shannon entropy (H)	Gini-Simpson index (D')	Evenness (H/H_{\max})	Effective species (\exp^H)
Mean	M: 23.25 \pm 5.965 S: 27.00 \pm 4.183	M: 224.3 \pm 42.67 S: 350.0 \pm 107.7	M: 2.092 \pm 0.356 S: 2.048 \pm 0.281	M: 0.722 \pm 0.099 S: 0.721 \pm 0.0819	M: 0.661 \pm 0.092 S: 0.628 \pm 0.0866	M: 9.739 \pm 3.270 S: 8.659 \pm 2.184
ANOVA results	df					
Habitat	1,6	0.701	0.517	0.470	0.281	0.445
Flight	2	0.725	0.252	0.271	0.251	0.217
Habitat x Flight	2	0.525	0.038	0.071	0.106	0.166
Holm-Sidak contrasts						
1) Flight within Remnant	no	no	no	no	no	no
2) Flight within Restored	no	no	no	no	no	no
3) Habitat within Flight	no	no	no	no	no	no

Notes: Habitat refers to remnant and restored prairie sites. Flight refers to flight period (early-, (E), mid-, (M), and late-season (L)), which correspond to capture month (June, July and August). Contrasts of site means were evaluated by the Holm-Sidak method of multiple comparisons with an overall significance level of 0.05.

Table 2.8. Indicator species analyses for wild bees from different grassland habitat types within three study locations in Nebraska. Monte Carlo tests of significance on maximum indicator values (IV) are listed, as well as the mean IV, for CRP, remnant prairie, and grazed pasture within the Southeast Prairies BUL, remnant prairie and restored prairie within the Platte Prairies, and high and low diversity plantings (CP42 and CP25, respectively) within the Holt CRP site. Standard error is given in parentheses.

Bee species & Location	Habitat/Planting (max)	IV	Mean (s.d.)	<i>p</i> -value
Southeast Prairies BUL				
<i>Anthophora walshii</i>	CRP	62.5	45.5 (6.60)	0.0166
<i>Apis mellifera</i>	CRP	93.0	90.7 (1.70)	0.0236
<i>Diadasia enavata</i>	CRP	60.3	48.5 (5.54)	0.0174
<i>Halictus ligatus</i>	CRP	66.8	45.0 (10.68)	0.0522
<i>Lasioglossum nymphaearum</i>	Prairie	56.8	29.2 (12.92)	0.0416
<i>Melissodes agilis</i>	CRP	57.4	49.3 (6.87)	0.0440
<i>Melissodes bimaculata</i>	CRP	57.3	42.2 (4.86)	0.0058
<i>Melissodes coloradensis</i>	CRP	61.8	39.0 (10.29)	0.0400
<i>Melissodes comptoides</i>	CRP	48.4	40.9 (4.12)	0.0564
Holt CRP				
<i>Agapostemon angelicus</i> *	Low diversity	69.2	49.0 (8.16)	0.0276
Platte Prairies				
None	--	--	--	--

Notes: Habitat/Planting (max) indicates the habitat or planting type in which the maximum indicator value (IV) was observed within each study location. The *p*-values listed represent the proportion of 4999 randomized trials in a Monte Carlo simulation in which indicator values equal or exceed the observed indicator value. A small *p*-value indicates that a species is more abundant and constant in a habitat or planting type than would be expected by chance.

**Agapostemon angelicus* and *A. texanus* females cannot be distinguished using morphological characters in populations west of the Mississippi River.

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CHAPTER 3: THE FUNCTIONAL COMPOSITION OF PRAIRIE BEE ASSEMBLAGES IN RELATION TO FLORAL RESOURCE AVAILABILITY

ABSTRACT

In grassland ecosystems, greater species diversity in plant-pollinator networks can translate into greater complexity and stability in community structure because of overlap and complementarity in the functional roles of community members. The diversity and composition of species' functional traits determine ecological functioning and reduced biodiversity can weaken function. In this study I characterized the functional composition of wild bee assemblages from three types of natural and semi-natural grasslands in an agriculturally fragmented tallgrass prairie landscape in southeastern Nebraska. Species were categorized into functional guilds according to sociality, nesting strategy, floral specificity, body size, and foraging capacity. The composition of assemblages from properties enrolled in conservation reserve program (CRP), grazed pasture, and remnant prairie (haymeadow) were then compared on the basis of species, functional guild, and trait distributions among these habitats. Several functional diversity metrics were also employed to explore how traits are distributed among species using a multiple trait approach to diversity assessment. The importance of blooming forb abundance, species richness, and diversity was also assessed for each level and resource utilization was assessed via correspondence of pollen types from captured bees and available resources within each habitat. Species diversity estimates of wild bees were greatest for CRP habitats but composition was similar among the three types of grasslands in terms of species, functional guilds, or the distribution of traits. These

appear to be driven more by floral resource availability as suggested by the correspondence of pollen-bearing bee abundance and pollen types to blooming forb abundance, species richness, and diversity. Functional richness of the bee community also increases with forb diversity, which may be interpreted as a greater area of niche space being occupied where diverse floral resources are more available. Large social species were more abundant than other functional guilds across habitat types and comprised the majority of pollen-bearing bees, suggesting that these species have a dominant role in providing pollination services and may be favored in this landscape. The diversity of bees in CRP, the diversity of forbs in remnant prairie, and the proportion of bees collected with pollen loads corresponding to the pollen profile of forbs in remnant prairie suggest complimentary habitat use by wild bees with the capacity to forage at least moderate distances between habitats. All three habitat types examined here exhibit a rich assemblage and support species from all functional guilds. A trait-based approach which incorporated pollen analysis as a proxy of resource utilization was useful in this study because it helped identify which guilds and in which habitat types bees carry out the bulk of pollination services among these grasslands. Future work may build upon this by identifying whether functional compensation or replacement occurs in other contexts where whole suites of species and entire guilds have declined.

INTRODUCTION

Biodiversity is most simply described as the number of different species within a given area but ultimately, it is used to represent heterogeneity of organisms or their traits. Species are often placed in functional categories by physiological and morphological traits and previous work has done this for both plants (Tilman et al. 1997; Fargione and Tilman 2005) and pollinators (Fontaine et al. 2006). The definition of traits and their use as functional components of ecology has been controversial, particularly for plants (Violle et al. 2007), but this approach has been successful for wild bee communities using life-history categories to represent functional components of diversity (Kennedy et al. 2013; Ekroos et al. 2013; Hoiss et al. 2012).

It is the diversity and composition of species' functional traits in a community that determine ecological functioning (Cadotte et al. 2011), and reduced biodiversity can weaken function (Balvanera et al. 2005; Hooper et al. 2012). In grassland ecosystems, greater diversity in the species of plant-pollinator networks can translate into greater complexity and stability in community structure because of overlap and complementarity in the functional roles of community members. This means that the loss or decline in one species that performs a particular functional role may be compensated for by other species with overlapping roles (Travers et al. 2011, Hoehn et al. 2008), or that diverse communities function more efficiently (i.e. utilize resources more efficiently in space and time) than low diversity communities (Cardinale et al. 2006; Hooper et al. 2005; Fontaine et al. 2006). Regarding pollination function, the level of pollination within a plant community corresponds to the abundance and species richness of pollinators (Kremen et al. 2002; Klein et al. 2008; Slagle and Hendrix 2009). Although arguments have been

presented that conservation of a few dominant species, rather than diversity as a whole suite of common and rare species, is sufficient to maintain ecosystem functioning (see Schwartz et al. 2000), in typical ecological communities, most species occur in low abundances (Rabinowitz et al. 1986; Howe 1999) and therefore, many rare species may aggregately have a significant role in ecosystem functioning (Lyons and Schwartz 2001; Lyons et al. 2005).

Although corresponding changes in species and functional trait diversity may occur simultaneously, the functional guilds of a community may not be affected equally by environmental change (Flynn et al. 2009; Mayfield et al. 2010). Previous research has shown that traits such as body size or diet specificity influence how species respond (Williams et al. 2010; Rader et al. 2014). Bee response to agriculture, for example, does not consistently indicate harm by this conversion of natural habitat (Tscharntke et al. 2005; Winfree et al. 2009; Williams et al. 2010). Some species may actually benefit from certain practices (Cane 2008; Julier and Roulston 2009). However, many aspects of bee functional diversity are not well supported in agroecosystems, especially for species with above-ground nesting behaviors, and so maintaining natural habitat is important for retaining, and enhancing, the functional diversity of wild bee communities in these landscapes (Forrest et al. 2015).

Heterogeneity in resource availability among and within the habitat patches of a landscape can also act as environmental filters to bee species' distributions by life-history traits (Sydenham et al. 2015). For instance, the landscape level reduction of resources that accompanies land use change has contributed to declines in bumble bees and other

wild bees (Kremen et al. 2002; Tscharntke et al. 2005; Ollerton et al. 2014; Goulson et al. 2015; Potts et al. 2015). At the local scale, differences in species' perceptions of resource quality can influence foraging behavior, but regardless of scale, both the quantity and the quality of floral resources matter for bee health. Diversity of floral resources ensures proper nutrition for sufficient development and reproduction, both of which are needed for populations to persist in a landscape (Vaudo et al. 2015). Obtaining these nutrients often requires foraging on complementary food sources and strongly influences foraging behaviors and fitness (Behmer 2009), but specific requirements differ among bee species (Vaudo et al. 2015). For example, the quantity of pollen used to provision the brood of some solitary bees has been shown to be linearly correlated to body size (Müller et al. 2006) and in specialist species, non-host pollen results in poor development and survival (Praz et al. 2008). Also, local flower abundance has been shown to have a significant positive effect on bee species richness in landscapes with few natural habitats (Hines and Hendrix 2005; Kleijn and Langevelde 2006), and bees shift activity among habitats in response to resource availability (Mandelik et al. 2012).

Because forb species differ considerably in the quality of pollen and nectar (Roulston and Cane 2000; Nicolson and Thornburg 2007), this can influence the choices foraging bees make regarding which species of forbs to visit to meet nutritional needs. Some species of bees have been shown not only to prefer pollen with higher essential amino acid concentrations (Cook et al. 2003; Somme et al. 2014; Konzmann and Lunau 2014), but may collect pollen from diverse sources in order to obtain sufficient balance of amino acids (Weiner et al. 2010) and lipids to meet their dietary needs (Vaudo et al. 2015). Similarly, long-tongued and short-tongued bees differ in their preferences of

sugar composition (Baker and Baker 1983) and visit different types of forbs. A diverse forb community, therefore, is better equipped to meet the needs of a diverse wild bee community.

The aim of this study was to examine the functional composition of the wild bee assemblages of natural and semi-natural grasslands in an agriculturally fragmented tallgrass prairie landscape in Nebraska and explore the importance of floral resource availability to the distribution of bee functional traits in this context. I addressed three general questions: (i) do the wild bee assemblages of different grasslands differ in the composition of species or functional traits, (ii) is functional composition or diversity correlated with floral resource availability, and (iii) does the composition of pollen collected by bees correspond to available floral resources and therefore indicate resource utilization in these grasslands? Such information is valuable to conservation planning as it can reveal how bees use habitats of different quality, and then guide decisions on which habitats to maintain or enhance with floral resources to encourage diversity within the wild bee community. This may help to ensure sufficient pollination services among the remnants of a fragmented prairie ecosystem.

METHODS

Study area and sites

The study location consists of an agricultural landscape in southeastern Nebraska, with specific study sites in Johnson, Pawnee, and Richardson Counties. All sites were located within an area designated by the Nebraska Natural Legacy Project as a Biologically Unique Landscape (BUL), this one being the Southeast Prairies BUL. A

total of 15 sites were selected from three of the dominant grassland types in the landscape: remnant tallgrass prairie (also referred to as haymeadow), grazed pasture, and properties enrolled in the Conservation Reserve Program (CRP). Five privately owned properties were selected for each grassland type based on management practices and landowner permission. The remnant prairies were managed for hay production, with haying occurring once per year. The grazed pastures were actively grazed by cattle during the study, although cattle were rotated between different pastures at different times. The CRP properties were all CP25 grass/forb seed mixes at least five years into their CRP contract. These natural and semi-natural grassland patches were sampled as representatives of different suitable bee habitat types within a mosaic of row crop agriculture (predominantly corn or soybeans), woodlands, and grasslands. Sites were each sampled twice in June, July, and August of 2012, and at least once in each of the same months in 2014 with the exception of two CRP sites that had been converted back to row crop production after the first year of the study and were therefore not available for further sampling. The size range of these study sites was 7.6-58.4 acres.

Bee sampling and identification

The wild bee assemblages were sampled with blue vane traps (SpringStar® Inc., Woodinville, WA, USA) suspended from a PVC pole at the level of the vegetation. Traps were set up for 48 hours during appropriate weather conditions, with four traps in each site, placed at least 30 meters apart. Bees were transferred from the traps to Ziploc® freezer bags in the field, then placed in a freezer until specimens could be sorted and identified. Bees were identified to species when possible but some groups, such as

Lasioglossum, were frequently identified only to genus or to morphospecies.

Agapostemon angelicus (Cockerell, 1924) and *Agapostemon texanus* (Cresson, 1872) were considered the same species in this study since females cannot be distinguished based on morphological characters in populations west of the Mississippi River. Bees were first identified to genus using Michener et al.'s Bee Genera of North and Central America (1994) and then to species using a combination of keys on discoverlife.org, local keys to prairie bees of Missouri and a reference collection with confirmed species identifications that was created with professional assistance from Mike Arduser at the Missouri Department of Conservation, St. Louis Regional Office, St. Charles, MO, 63304 USA. Information on bee functional traits was obtained from the same resources.

Characterization of the bee community using natural history traits

Overall abundance, species richness, and the Shannon diversity index were calculated for each sample day. Abundance is the sum total of individuals collected at the four blue vane traps at each site and is a relative measure for each site rather than an estimate of all bees at a site. Species richness is the total number of species collected from each site. Although Shannon diversity is calculated from both the number of species and their relative abundances, it is useful because it characterizes the evenness of the community. Additionally, bee species were divided to categories according to certain functional traits: sociality, nesting strategy, floral specificity, body size and foraging capacities (Appendix G).

Sociality describes either *social* species or *solitary* species. Only eusocial species with a queen as the only egg-laying female were considered *social*, and these were

further categorized as *large* or *small social* species. Intermediate degrees of sociality, such as gregarious and other communal nesting behaviors, were not considered social in this study. *Solitary* species construct a nest and provision their own offspring with food. *Cleptoparasites* were considered as a separate group under nesting strategy rather than sociality since these species locate the nests of suitable hosts and lay eggs to be provisioned by the nest-building species. Other nesting strategies included *cavity-nesters*, *ground-nesters*, and *wood-nesters*. *Cavity-nesting* species are hypergeic (above-ground) or endogeic (below-ground; Oertli et al. 2005) and nest in existing natural cavities (Michener 2007). *Ground-nesting* species are endogeic and excavate nests in the soil. *Wood-nesting* species are hypergeic and use wood or twigs to construct their nests. Wood-nesters were additionally categorized as *large* and *small* wood-nesting species. *Augochlora pura* was considered a wood-nesting species although it doesn't excavate because it creates a nest under bark.

Floral specificity was defined as either *polylectic* or *oligolectic*. *Polylectic* bees are generalists and forage on numerous, unrelated forbs for pollen and *oligolectic* bees are limited to certain, typically related, pollen taxon (Michener 2007). Other degrees of pollen specialization, such as monolecty, were not distinguished from oligolecty. Most species exhibit a range in body size within a few millimeters, although the most extreme polymorphisms are those of bumble bee workers (Couvillon et al. 2010; Jandt and Dornhaus 2014), so maximum body size was categorized into five groups: $\leq 8\text{mm}$, 9-12mm, 13-16mm, 17-20mm, and 21-27mm. Finally, species were assigned to broad foraging capacities which span the range of distances for solitary bees in relation to intertegular distance as described by Gathmann and Tschardtke (2000), and for body

length as summarized by Zurbuchen et al. (2010). These included doorstep foragers (up to 250m from nest), short- to moderate-distance (250m-400m), moderate-distance (400m-800m), and two long-distance foraging categories: 800m-1200m, and greater than 1200m from the nest.

Community diversity measures

Several measures were used to compare the bee assemblages between the different habitat types. These were species richness, abundance, evenness, Shannon entropy, and Simpson dominance. Evenness was included as a complement to Shannon entropy and species richness. It was measured as H/H_{\max} , where the H is Shannon entropy and H_{\max} is its maximum value ($\ln[\text{species richness}]$). Shannon entropy is also referred to as the Shannon-Wiener diversity index and hereafter described as Shannon entropy or Shannon diversity for simplicity and to keep terminology consistent. Simpson dominance was measured as the Gini-Simpson index, which measures the probability of interspecific encounter (Hurlbert, 1971) and is calculated by $1 - \lambda$ (where λ is the original Simpson index which indicates the probability that any random two individuals will be of the same species). Two diversity indices were used because each accounts for dominant and rare species differently and, therefore, depicts slightly different aspects of species composition. Effective species measures were calculated by taking the exponential of Shannon entropy for each site. Data were converted to individuals per study site per sample day to account for discrepancies between CRP and the other habitat types following the loss of certain study sites after the first season, and data were pooled from each season.

Functional guilds and diversity estimates

The functional diversity of the wild bee assemblages was assessed by first determining the number of functional categories. Cluster analysis was used to determine the best assignment of species into guilds (Pla et al. 2012) based on 5 traits and 23 modalities (Table. 3.1); the five “traits” were maximum body size, foraging capacity, breeding strategy, nesting behavior, and floral specificity (trait profiles and guild assignments for each species are provided in Appendix G). Clustering of species was based on a dissimilarity matrix on standardized data where weighted differences cluster in ‘trait space’ with the Jaccard method. The number of clusters began at 5 but was increased until the heterogeneity of species’ traits was reduced to the point that species with the same primary natural history traits (breeding and nesting strategies, and floral specificity) clustered together. The final assignment of species into functional guilds (Figure 3.2) was then used in a correspondence analysis to examine the relationship of guilds and trait modalities to the three habitat types.

Additionally, five components of functional diversity were calculated for each study site and compared among the three habitat types. These included functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) as a means of describing the relationship of functional diversity to the environment (Mason et al. 2005). Functional richness is the multidimensional trait space that is filled by an assemblage of species, the boundaries of which are defined by species’ most extreme trait values (Villegier et al. 2008). It can be described as the niche space that is filled by the species of a community (Cornwall et al. 2006; Schleuter et al. 2010). It is often used as

an indicator of used niche space, which buffers against environmental fluctuations (Mason et al. 2005).

Functional evenness describes the regularity with which species' traits, weighted by relative abundances, occur in trait space (Villegger et al. 2008) and is used as an indicator of resource utilization, where a high index values indicate a regular distribution and low index values indicate separate clusters of species' traits (Schleuter et al. 2010). Functional divergence also measures how trait space is filled (Schleuter et al. 2010), but it quantifies the spread of species from the community centroid (Villegger et al. 2008) and can detect predominance of extreme species when clusters form away from this centroid (Mason et al. 2005).

Functional dispersion (FDis), is the average distance, in multidimensional trait space, to the abundance-weighted centroid and is used as a compliment to the first three as a measure of beta diversity (Laliberté and Legendre 2010). Similarly, Rao's quadratic entropy (Q), the fifth metric, is the abundance-weighted variance in traits (Botta-Dukat 2005; Rao 1982) and summarizes both functional richness and divergence. It is useful in that it can be broken down to component parts of alpha-, beta-, and gamma-diversity (Mouchet et al. 2010; Villegger and Mouillot 2008). All functional diversity measures were calculated with the software program FDiversity (Casanoves et al. 2010) using a multi-trait approach. Multiple components of functional diversity were used here to gauge which may better indicate potential drivers of bee distributions, as a proxy to pollination services. The total volume of trait space that is occupied by the species of a

community might affect ecological processes differently than the packing of species within that space (Clark et al. 2012).

With this examination I made comparisons between habitat types at three levels of bee diversity: 1) at the species level, 2) among functional guilds to which species were assigned based on trait profiles, and 3) when the assemblages of species are described by the distribution of trait modalities among species.

Floral resource availability and resource utilization

The association of bee community variables to floral resource availability was also assessed at all three levels. Floral resource availability was measured in terms of bloom abundances and the number of forb species in bloom. Bloom abundance was estimated by counting the number of blooming stems for each blooming species within 2 circular plots, each $\frac{1}{4}$ acre in size (1,012 m²). The number of flowering ramets has been used as a reasonably accurate proxy of floral resources when sampling over large areas at many sites (Hines and Hendrix 2005). Forb sampling locations were randomly selected for each study site prior to each session but were never overlapping. Forb sampling occurred simultaneously with bee sampling, although an additional day was taken when needed at sites where forb density was high. Forb species richness and abundance were recorded for each site, from which density (blooming stems per m²) was estimated.

In addition to information on the number and types of forbs in bloom (Appendix H) at the time of trapping, pollen was collected from the bees themselves and used as a gauge of actual resource utilization. Females were examined for the presence of scopal or corbicular pollen upon sorting and identification, and both the total number of females

with pollen loads and the proportion of females with pollen loads were recorded. Select samples were also processed through acetolysis to explore the similarity of the pollen profiles (Appendix I) to the locally-available forb community.

For acetolysis, the bee carcasses of three species (*Bombus auricomus*, *Eucera hamata*, and *Agapostemon virescens*) which were abundant in all sites were separated from other species collected during the second sampling session in June and the first session of August and used as representatives of foraging bees from each site. Specimens were bathed in 95% EtOH and sonicated for 30 seconds. The resulting pollen solutions were transferred to 3-dram glass vials and stored in the refrigerator to await acetolysis. To prepare the samples for processing, the vials were sonicated for 15 seconds to restore the suspension of pollen grains and an aliquot of each solution was transferred to a 2ml conical microcentrifuge tube. A single Lycopodium spore tablet (Batch #124961), containing approximately 12,500 spores, was dissolved in hydrochloric acid and an aliquot was added to each solution. Each sample was then centrifuged, the EtOH was decanted, and glacial acetic acid was used as a rinse prior to acetolysis. The acetolysis solution (consisting of 9:1 acetic anhydride:sulfuric acid) was added and the samples were placed in a hot water bath for five minutes. Following centrifugation, the used acetolysis solution was decanted and each sample was washed with glacial acetic acid on a vortex genie. The samples were centrifuged again, decanted, and finally, washed with distilled water.

Pollen analysis then began by preparing pollen slides for each sample which could be compared to a pollen library that was constructed with pollen samples taken

directly from the forbs and processed in the same manner. An aliquot of the processed solution for each sample was mixed thoroughly with a drop of glycerin on glass microscope slides and covered with glass coverslips. Nail lacquer was used to seal the samples prior to light microscopy, during which pollen grains were counted and identified. The pollen concentration values were then calculated by multiplying the ratio of pollen grains counted to Lycopodium spores counted by the number of Lycopodium spores added to each solution ($(\# \text{ pg}_{\text{counted}} / \# \text{ Lsp}_{\text{counted}}) * \# \text{ Lsp}_{\text{added}}$). Pollen types were identified to species when possible, using the pollen library of local forbs as well as the expertise of the University of Nebraska-Lincoln Palynology Lab. Most pollen was identifiable to at least the family level and this information was recorded along with the calculated concentration for each sample. Pollen types were further categorized by plant type: herbaceous forbs, grasses, or woody growth forms (trees or bushes). The pollen profiles of each specimen were pooled for each of the 15 study sites.

Statistical analyses

A one-way analysis of variance with Holm-Sidak multiple comparisons test was used to examine differences between habitat types in bee species richness, abundance, evenness, diversity estimates, and effective species. Shapiro-Wilk normality tests and Brown-Forsythe equal variance tests were applied for all variables. Nonmetric multidimensional scaling (NMS) was used to visualize differences in bee species compositions based on a matrix of relative Sørensen dissimilarities, and the significance of differences was tested with multi-response permutation procedures (MRPP; PC-ORD version 6, MjM Software). The MRPPs compare differences among and between groups

based on the average within-group similarity and the probability of obtaining the observed average within-group distance is used as a p -value (Peck, 2010). The ordinations and MRPP tests were repeated after converting the data matrices to presence-absence data to assess whether the differences in communities were a consequence of species' identities or relative abundances, since similar results with both data formats suggest the importance of species composition in explaining differences between sites and locations. These procedures were repeated for the blooming forb community.

To test for differences in the functional composition of the wild bee community either a one-way ANOVA or a Kruskal-Wallis H test was performed for each of the 10 guilds into which species were categorized during cluster analysis, and again for each modality type within each trait. Holm-Sidak and Tukey contrasts were used to compare guilds and modalities between and within each grassland type. Finally, these tests were again applied to the functional diversity indices to test whether any measure was significantly higher or lower in one habitat type than another. These analyses were repeated using the abundance data for pollen-bearing bees, both overall and within functional categories.

Shared species and community similarity were assessed between habitat types for both the bee and forb communities using EstimateS. Similarity was measured as Sørensen similarity (1-Sørensen distance). For bees, this was done for species, functional guilds, and trait modalities. For forbs, this was done for blooming forbs and pollen types. Mantel tests (PC-ORD version 6.0, MjM Software) were performed to determine the nature of associations, if any, between the bee and forb communities. Bee species,

functional guilds, trait modalities, all pollen-bearing bees, and pollen-bearing bees within functional guilds were tested for associations to blooming forbs and pollen types. All tests used 999 randomized runs on relative Sørensen distances.

Pearson product moment and Spearman rank correlations were also conducted to examine the relationships between the bee and forb communities. These were done in SigmaPlot 13.0 (Systat Software, San José, CA). Spearman rank correlations were performed for functional richness (FRic), the proportion of pollen-bearing bees, blooming forb density, and forb diversity indices. All other parameters were tested with Pearson product moment correlations since the assumptions of normality and equal variance were met. Finally, indicator species analysis (ISA; PC-ORD version 6, MjM Software) was used to determine which species, functional guilds, trait modalities, forb species and pollen types are most distinguished within the bee and forb communities of each habitat type.

RESULTS

A total of 8,016 bees from 82 species, 33 genera and all 5 families were collected from the 15 study sites of the Southeast Prairies Biologically Unique Landscape. The 38% collected from CRP habitats represented 67 species from 29 genera, 7 of which were unique to this habitat type and represented by a single individual. The most commonly collected species were *Melissodes comptoides* (328 individuals), *Eucera hamata* (326 individuals), and *Augochlorella aurata* (224 individuals). The 26% collected from grazed pasture represented 58 species and 24 genera. Like the unique species of CRP, each of the six unique species found in grazed pasture were singletons. The only records

of *Bombus fervidus* (Fabricius, 1798), *Megachile sculpturalis* (Smith, 1853), and *Xenoglossa strenua* (Cresson, 1878) in this study came from this habitat type. The most commonly encountered species were *Agapostemon virescens* (269 individuals), *Melissodes comptoides* (193 individuals), and *Bombus pensylvanicus* (180 individuals). The remaining 36% of bees collected were the 64 species and 26 genera from the remnant prairie sites. This habitat type contributed six unique species to the overall assemblage, three of which were singletons, and included *Ceratina calcarata* (Robertson, 1900), *Habropoda morrisoni* (Cresson, 1878), *Nomada affabilis* (Cresson, 1878), and *Nomia universitatis* (Cockerell, 1908). The most commonly collected species of remnant prairies were *Agapostemon virescens* (544 individuals), *Eucera hamata* (322 individuals), and *Bombus pensylvanicus* (251 individuals).

Community diversity measures

Neither abundance nor species richness of the bee community differed between habitat types (Table 3.2). Bee species evenness was greatest in grazed pasture (0.785 ± 0.020) and least in remnant prairie (0.729 ± 0.012), and although the ANOVA detected significant differences between habitats ($F_{2,12} = 4.287$, $p = 0.039$), multiple comparisons were only approaching significance for these habitats ($p = 0.064$). Shannon entropy was greater in CRP sites than remnant prairie ($F_{2,12} = 5.991$, $p = 0.016$). The magnitude of difference between CRP and prairie (effective species) was also significant ($F_{2,12} = 5.930$, $p = 0.016$). Simpson dominance was greater in both CRP and pasture sites than prairie ($F_{2,12} = 8.091$, $p = 0.006$).

There was considerable overlap in species composition between study sites (Figure 3.1). The NMS ordination using species abundance data was a two-dimensional solution that explained 84.7% of variation (64.7% on the first axis and 23.0% on the second). When repeated on presence-absence data, the ordination became a one-dimensional solution that explained 22% less variation (62.0% on a single axis). Results of the MRPP reflected the overlap in species between habitat types (Table 3.3). Within-group agreement was not stronger than between-group with either the abundance or presence-absence data format ($A = 0.012$, $p = 0.287$ and $A = 0.003$, $p = 0.406$, respectively).

Functional guilds and diversity estimates

In cluster analysis, bee species were categorized into 10 functional guilds based on trait profiles (Figure.3.2). The cophenetic correlation of the final dendrogram was 0.970, based on 601 species occurrences across the 15 study sites. The largest group of species was the ground-nesting generalists (Gnd.Ply (GP)) which comprised 39.5% of the bees collected from the study area (Table 3.4). Large, social, long-distance foragers (L.Soc.LDF (LS)) were the next most numerous guild, with 18.2% of individuals, but there were only eight species. These were followed by solitary ground-nesting sweat bees (Sol.Gnd (SG)), with five species and 17.5% of individuals. The next most specious guilds, oligolectic ground-nesters (Sol.Gnd.Olg (GO)) and small wood-nesters (Sol.Wd (SW)) comprised 9.4% and 2.1% of individuals, respectively. The remaining wood-nesters were either large wood excavators (Lg.Wd (LW)) or oligolectic wood-nesting species (Sm.Wd.Olg (WO)). No social parasites were collected in this study so

cleptoparasitic species were divided only into parasites of solitary ground-nesters (ML.Clepto (MC)) and solitary wood-nesters (SM.Clepto (SC)). The remaining species were social ground-nesters (Sm.Soc.GMF (SS)).

Few associations were inferred from correspondence analysis between functional guilds and habitat types (Figure 3.3). The strongest was for oligolectic wood-nesters and grazed pasture, which plotted in the same direction from the origin as pasture and the majority of pasture sites. The biplot of guilds and study sites explains 74.2% of variability (53.38% on the first axis and 20.82% on the second), while the biplot of guilds and habitat types explains all variation (95.44% on the first axis and 4.56% on the second). However, no significant differences between habitat types were detected with ANOVA or Kruskal-Wallis H tests using abundances within guilds (Table 3.5). Ground-nesting polylectic species (GP) were more numerous in CRP than pasture sites but the difference is only approaching significance (mean = 294.2 ± 46.02 , $F_{2,12} = 3.262$, $p = 0.078$).

Significant differences between functional guilds were found within each of the three habitat types (Table 3.6). In CRP sites, ground-nesting polyleges were more abundant than oligolectic wood-nesters and both groups of cleptoparasitic species, as were large social species. Solitary ground-nesting oligolectic species were more abundant only than wood-nesting oligoleges ($H = 44.171$, $df = 9$, $p < 0.001$). Within grazed pasture, ground-nesting polyleges and large social species were also more abundant than cleptoparasites and wood-nesting oligoleges, while solitary ground-nesting sweat bees were more numerous than both groups of cleptoparasites ($H = 43.329$, $df = 9$,

$p < 0.001$). Within remnant prairie sites, the ground-nesting generalists were again more abundant than cleptoparasites and wood-nesting oligoleges, as were the solitary ground-nesting sweat bees, although large social species were more numerous than the cleptoparasites of wood-nesting species and wood-nesting oligoleges, but not the cleptoparasites of solitary ground-nesting bees ($H = 44.154$, $df = 9$, $p < 0.001$).

Most trait modalities did not statistically differ between habitat types either and the distributions of each are summarized in Figure 3.4. Only one modality within each of two traits, body size and foraging capacity, differed between any habitats. Bee species with a maximum body size between 13mm and 16mm were more abundant in CRP than grazed pasture ($H = 6.720$, $df = 2$, $p = 0.035$). Bees with an estimated foraging capacity between 400m and 800m were also more often collected from CRP sites than pasture sites ($F_{2,12} = 5.218$, $p = 0.022$). All other trait modalities were similarly distributed among habitat types.

All traits differed within each habitat type, with at least one modality more prevalent than another (Figure 3.4). For body size, bees between 13mm and 16mm were more abundant than species with maximum body size of 8mm or less in CRP ($H = 12.251$, $df = 4$, $p = 0.016$) and grazed pasture ($H = 12.679$, $df = 4$, $p = 0.013$). Within prairie, however, species between 9mm and 12mm were more numerous than those 8mm or less ($F_{4,20} = 3.956$, $p = 0.016$). For foraging capacity, doorstep foragers (250m) were less frequently collected than species with an estimated range of 800m in CRP ($H = 11.269$, $df = 4$, $p = 0.024$) and pasture ($H = 12.254$, $df = 4$, $p = 0.016$), but were less abundant than species with a foraging capacity of 400m in prairie ($F_{4,20} = 3.930$, $p =$

0.016). Large social species and solitary species were more numerous than gregarious species in all habitats (CRP: $H = 22.526$, $df = 4$, $p < 0.001$; PAS: $H = 22.518$, $df = 4$, $p < 0.001$; PRA: $H = 22.547$, $df = 4$, $p < 0.001$). Solitary species were also more abundant than cleptoparasites in all habitats. Ground-nesters were more abundant than cleptoparasites in all habitats (CRP: $H = 16.714$, $df = 3$, $p < 0.001$; PAS: $H = 17.167$, $df = 3$, $p < 0.001$; PRA: $H = 16.727$, $df = 3$, $p < 0.001$), which also meant that species with below-ground nest locations were more numerous than those with no nests (CRP: $H = 12.02$, $df = 2$, $p = 0.002$; PAS: $H = 12.128$, $df = 2$, $p = 0.002$; PRA: $H = 12.522$, $df = 2$, $p = 0.002$). Finally, polylectic species were more abundant in all habitats than oligolectic species (CRP: $H = 6.818$, $df = 1$, $p = 0.008$; PAS: $H = 6.860$, $df = 1$, $p = 0.008$; PRA: $F_{1,8} = 128.893$, $p < 0.001$).

Functional diversity indices were also similar among all habitat types (Figure 3.5). The pasture study sites had the highest, albeit marginal, average functional diversity scores for most indices. These included Rao's quadratic entropy (0.754 ± 0.026), functional richness (0.456 ± 0.099), functional divergence (0.866 ± 0.012), and functional dispersion (0.727 ± 0.018). CRP had the highest functional evenness (0.332 ± 0.016), but the lowest Rao's quadratic entropy (0.704 ± 0.025), functional richness (0.295 ± 0.045), and functional dispersion (0.680 ± 0.028). Therefore, traits are more evenly distributed among species in CRP, but less niche space is occupied. Prairie was between pasture and CRP for all functional diversity indices except functional evenness (0.320 ± 0.008) and functional divergence (0.840 ± 0.021), for which it had the lowest average values, indicating that species are more clustered in trait space.

Floral resource availability and utilization

The forb community exhibited stronger differences between habitat types (Table 3.7). Forb species richness was greater in remnant prairie than both CRP and grazed pasture ($F_{2,12} = 8.700, p = 0.005$). The abundance of blooming forbs was greater in remnant prairie than in grazed pasture, but not CRP ($H = 6.500, df = 2, p = 0.039$). The forb community partitioned fairly neatly into groups that correspond to habitat type, with some overlap between pasture and CRP, and with prairie communities forming the most distinct cluster in species space (Figure 3.6). The ordination is two-dimensional and explains 76.7% of variation, 35.7% on one axis and 41% on the other. When the ordination was repeated after converting the data to presence-absence format the ordination remains a two-dimensional solution and explains 88.4% of variation, 72.3% on axis 1 and 16.1% on axis 2. In the MRPP, within-group agreement was much stronger than between-group agreement for blooming forbs (Table 3.8). CRP composition did not differ from pasture ($A = 0.0331, p = 0.101$) but the composition of forbs in prairie was different from both CRP ($A = 0.155, p = 0.007$) and pasture ($A = 0.167, p = 0.004$).

The 264 pollen-bearing bees that were collected were distributed differently among the three habitat types (Figure 3.7). Pollen loads were more often noted for bees from prairie sites than both CRP and pasture (PRA mean = 33.0 ± 3.56 , $F_{2,12} = 18.13, p < 0.001$), but a similar number of bees bore pollen in CRP and pasture habitats (means = 10.0 ± 2.83 and 9.8 ± 2.96 , respectively). *Bombus pensylvanicus* was the most common pollen-bearing species, with 93 individuals comprising 35.2% of pollen-bearers (Table 3.9). It was followed by *B. auricomus*, with 59 bees and 22.3% of pollen-bearers, so

collectively, these two bumble bees account for over half of the specimens with pollen. *Eucera hamata* was a close runner up, with 55 individuals and 20.8% of pollen-bearing bees, while *Agapostemon virescens* accounts for less than half of that, with 23 bees and 8.7% of the pollen-bearers. All of these species were collected in greater numbers from prairie sites.

Within each habitat, only the social long-distance foragers had significantly greater numbers of pollen-bearing individuals than other functional guilds (Table 3.10). Within CRP, more large social bees bore pollen than ground-nesting polyleges, and small and large wood-nesting polyleges ($H = 11.227$, $df = 4$, $p = 0.047$). Those of the grazed pasture habitats were greater in number than the small and large wood-nesters as well as the solitary ground-nesters ($H = 18.100$, $df = 4$, $p = 0.003$). Within prairie habitats, more large social bees bore pollen than small social bees, and large and small wood-nesting bees ($H = 19.172$, $df = 4$, $p = 0.002$).

Comparisons of Sørensen similarity values between habitat types revealed little difference between bee and forb communities (Table 3.11). Pasture and prairie habitats were more similar (60 species, Sørensen similarity = 0.77 ± 0.01) than either CRP and grazed pasture (50 species, 0.75 ± 0.01) or CRP and remnant prairie (55 species, 0.75 ± 0.01). The number of functional guilds and trait modalities differed only by one between habitat types. All guilds were shared between pasture and prairie (10 guilds, 0.91 ± 0.01), but not for CRP and prairie (9 guilds, 0.93 ± 0.02) or CRP and pasture (9 guilds, 0.90 ± 0.02). All trait modalities were shared between CRP and prairie (24 modalities, 0.96 ± 0.01), one less between CRP and pasture (23 modalities, 0.96 ± 0.01) and between

pasture and prairie (23 traits, 0.998 ± 0.001). CRP and prairie habitats were most dissimilar in terms of the blooming forb community (20 species, 0.34 ± 0.03), although pasture shared a similar number of species with both CRP (25 species, 0.45 ± 0.05) and prairie (26 species, 0.42 ± 0.03). Finally, the greatest number of shared pollen types was found between CRP and prairie habitats (19 types, 0.27 ± 0.03), followed by pasture and prairie (13 types, 0.22 ± 0.04), and CRP and pasture with the fewest (11 types, 0.27 ± 0.07).

Of the ten Mantel tests on the bee and forb communities, none showed a significant association (Table 3.12), and only the positive association between the number of pollen-bearing bees and the number of blooming stems was approaching significance ($r = 0.073$, $p = 0.061$). Pearson product moment and Spearman rank correlations detected more significant relationships between the two communities (Table 3.13), but only four correlations retained significance following Bonferroni correction for multiple comparisons. These included an increase in bee abundance with the abundance of blooming forbs ($r = 0.668$, $p = 0.0065$), and lower evenness and Simpson dominance at sites with greater forb species richness ($r = -0.602$, $p = 0.0175$ and $r = -0.681$, $p = 0.0052$, respectively). The ties between the bee and forb communities were further explored in supplemental comparisons by grouping study sites by similarity of species composition. These are shown by comparisons in bee and forb rank abundance curves in Appendix J, and with indicator species analyses in Appendix K.

The only functional diversity measurement with a significant association to the forb community in the correlation analyses was functional richness, which was greater at

sites with greater forb diversity calculated as Shannon entropy ($r = 0.536$, $p = 0.0382$), but the correlation was negligible after correcting for multiple comparisons (Table 3.13). In contrast, the number of pollen-bearing bees was significantly correlated to most of the measures of the forb community. The number and proportion of bees collected with pollen loads was greater at sites with higher blooming forb abundance ($r = 0.690$, $p = 0.0044$ and $r = 0.625$, $p = 0.0123$, respectively), density ($r = 0.777$, $p < 0.0001$ and $r = 0.625$, $p = 0.0123$, respectively), and forb species richness ($r = 0.798$, $p = 0.0004$ and $r = 0.888$, $p < 0.0001$, respectively). The proportion of pollen-bearing bees collected was also significantly greater from sites with higher forb diversity ($r = 0.511$, $p = 0.0498$). Following Bonferroni corrections, significance was retained in the correlations of pollen-bearing bees to blooming forb abundance, density, and species richness, but not diversity.

The indicator species analysis of the bee community gave nine species, one functional guild, and two trait modalities with significantly greater abundance and constancy to one habitat type over the others (Table 3.14). Each of these species was collected more often from CRP sites except for *Lasioglossum nymphaerarum*, which was most often collected from remnant prairie sites ($IV = 56.8$, $p = 0.0416$). No species were indicated as more constant to grazed pasture. No indicator values were perfect (100%) for any habitat type, but the highest was for the honey bee, *Apis mellifera*, which was collected most often at CRP sites ($IV = 93.0$, $p = 0.0236$). The other species indicative of CRP were *Anthophora walshii* (Cresson, 1869), *Diadasia enavata* (Cresson, 1872), *Halictus ligatus* (Say, 1837), *Melissodes agilis* (Cresson, 1878), *Melissodes bimaculata* (Lepeletier, 1825), *Melissodes coloradensis* (Cresson, 1878), and *Melissodes comptoides* (Robertson, 1898). Ground-nesting generalist species were more abundant and constant

to CRP sites than either remnant prairie or grazed pasture (IV = 41.4, $p = 0.476$), as were species with a foraging capacity of 800m and a maximum body size of 16mm (IV = 46.1, $p = 0.0154$ and IV = 49.8, $p = 0.0146$, respectively).

In contrast to the bee community, indicator species analysis of the forb community gave eleven forb species and nine pollen types that were constant to either remnant prairie or grazed pasture and none that were significantly more frequent in CRP (Table 3.15). Indicator values were also considerably higher for the forb community than those of the bee community. *Amorpha canescens*, *Linum sulcatum*, *Potentilla recta*, and *Psoraleidium tenuiflorum* each had perfect indicator values for remnant prairie (IV = 100.0, $p = 0.0008$), while the indicator value for *Verbena stricta*, the only blooming forb species that was significantly more constant to grazed pasture than other habitat types, was nearly perfect (IV = 97.8, $p = 0.0008$). The pollen of *Amorpha canescens* and *Potentilla recta* also had perfect indicator values for remnant prairie (IV = 1.000, $p = 0.0006$), although *Psoraleidium tenuiflorum* did not (IV = 853, $p = 0.0030$) and the pollen of *Linum sulcatum* was not indicative at all. *Verbena stricta* was also not specific to grazed pasture according to pollen types, although it was significantly more abundant and constant to it (IV = 0.866, $p = 0.0026$). Of the ten blooming forb species that were significantly more abundant and constant in remnant prairie, five were also among the significant pollen types for the same habitat. *Melilotus alba* pollen was more often identified on bees from grazed pasture (IV = 0.853, $p = 0.0050$) even though it was not significantly more abundant or constant among the blooming forbs of this habitat type. Similarly, pollen from *Ceanothus herbaceus* was more often identified from the bodies of bees that were collected from remnant prairie (IV = 0.877, $p = 0.0064$), although it was

not among those with significant indicator values for prairie forbs. The potential associations between species of bees and forbs given in these indicator species analyses were further explored with correlations and the results are shown in Appendix L. The two communities were also examined for seasonal differences in species composition (Appendix M), and supplemental comparisons sought the species driving those differences (Appendices N).

DISCUSSION

The different functional components of the wild bee community that were investigated here were well represented in the species assemblages from the Southeast Prairies BUL. Although diversity estimates were greatest for CRP habitats, composition ultimately did not differ between the three types of grasslands in terms of species, functional guilds, or the distribution of traits. These appear to be driven more by floral resource availability as suggested by the correspondence of pollen-bearing bee abundance and pollen types to blooming forb abundance, species richness, and diversity. Functional richness of the bee community also increases with forb diversity, which may be interpreted as a greater area of niche space being occupied where diverse floral resources are more available. However, large social species were more abundant than other functional guilds across habitat types and comprised the majority of pollen-bearing bees, suggesting that these species have a dominant role in providing pollination services and may be favored in this landscape.

Although the composition of species, functional guilds, and traits were equitable between habitat types, the greater number of medium-size bees (13-16mm) and moderate foragers in CRP may be due to more than half of the species in with these traits being ground-nesters. Most solitary bee species are ground-nesters (Mader et al. 2011) and so this group contributes substantially to the landscape's species pool. Diversity of wild bees in CRP may be partially explained by the availability of nesting substrate, particularly open ground at two large CRP sites, for bees with this nesting behavior. Native bees have been observed to nest in high numbers in CRP, especially at large sites (Wojcik *personal communication*), and in this study, bare ground may have provided nesting substrate to ground-nesting bees, including *Anthophora walshii*, *Diadasia enavata*, *Halictus ligatus*, and the four *Melissodes* species which were more abundant and constant in CRP than pasture and prairie.

Alternatively, the structural diversity hypothesis may partially explain the diversity of wild bees in CRP. In addition to bare ground at two large sites, other CRP sites were characterized by standing tall grasses because management restricts burning, mowing, and grazing in CP25 plantings. Vegetation in pastures and remnant prairie was typically shorter due to grazing activities and annual haying, respectively, even though the forb community of the latter still offers better quality forage. Because taller vegetation is more structurally diverse than short (Morris 1971; Lawton 1983), it offers greater niche space for species to occupy than shorter, intensively managed grasslands (Southwood et al. 1979; Morris 2000). However, functional richness of the wild bee community, which can be interpreted as the niche space that species fill (Schleuter et al.

2010), was positively correlated to a diverse forb community, which was far greater in remnant prairie habitats than CRP.

Because blooming forb abundance was not different between CRP and prairie, even though species richness and diversity were lower than prairie, the potential for these habitats to serve as important forage cannot be eliminated. However, because species with the capacity to forage as far as 800 meters from their nesting sites were abundant in CRP, and such species are not restricted to these resources, floral resources within this foraging distance in the surrounding landscape can also contribute to diversity of species collected within CRP sites. Moreover, although CRP may offer forage, recent studies have shown the importance of pollen quality and diversity for immune function in honey bees (Alaux et al. 2010) and native bees (Roulston and Cane 2002; Tasei and Aupinel 2008). The diversity and abundance of floral resources in remnant prairie may better satisfy these nutritional requirements and allow for sufficient reproduction and persistence of a diverse assemblage of species than CRP. Therefore, these natural and semi-natural habitat types may be used complementarily.

The data on pollen-bearing bees and pollen types provided some insight into resource use among habitat types. A greater proportion of large social species bore pollen at the time of collection than other guilds. Stephen and Rao (2007) observed that most individuals captured with blue vane traps did not carry pollen and concluded that capture occurred during the flight to find suitable forage, rather than on the return flight. Following the same logic, it's assumed here that bees bearing pollen were either captured during their return flight to the nest after foraging, or between flower visitations while

actively foraging. Thus, the greater number of bees with pollen loads collected in remnant prairie may suggest that these sites are preferred foraging destinations. This is supported by the correspondence of pollen types identified from the bees to the forb species in bloom at the time of collection.

Alternatively, this may be an artifact of the blue vane traps used in this study, and differences in the structure of vegetation between CRP and prairie sites. It should be noted that blue vane traps are not passive. Their reflective properties are highly attractive to flower-visiting insects, especially bees. Previous studies have noted that the proximity of traps to floral resources doesn't impact trap performance (Kimoto 2012, Stephen and Rao 2007), but because of the attractive nature of the traps, this study placed them within the vegetation, hanging at the same height as, rather than above, the surrounding plants. Still, although this is intended to reduce the attractive bias of the traps, it cannot also be assumed that the traps had not interfered with the foraging paths of captured bees, and therefore had some influence on the pollen-bearing bees observed in this study. In particular, traps were more visible in CRP sites with a lot of exposed ground than in any prairie sites. Therefore, the traps in those CRP sites may have operated as a beacon for foraging bees, initiating a bee-line, no pun intended, to the trap prior to visiting comparatively less attractive blooming forbs along the way.

It's important that sufficient resources are economically (i.e. energetically) attainable within the foraging capacities of bees (Cresswell et al. 2000) since, as central place foragers, bees carry pollen back from a foraging site to a nesting site where it is used to provision offspring. Otherwise, the heterogeneity of resource distribution can act

as an environmental filter, creating a nested composition of species by body size or foraging capacity. Instead, so long as sufficient nesting and forage resources are available within a variety of foraging ranges, a diverse suite of wild bees can use the natural and semi-natural grasslands of this landscape complementarily. Complementary habitat use has been documented in previous work (Mandelik et al. 2012), but an important limitation to the specific conclusions of habitat use in this study is that nest site availability was not quantified and directly tested. In a recent study, Forrest et al. (2015) found that functional dispersion of traits in an agroecosystem was only significantly greater in natural habitats than cultivated habitats when measures of nesting suitability to wild bees were considered. Still, flexibility in the foraging behaviors of wild bees in response to the distribution of resources in other agricultural mosaic landscapes has been documented, and it's reasonable to assume that the same phenomenon occurs in the Southeast Prairies. For example, Williams and Kremen (2007) compared the pollen types which *Osmia lignaria* used in the nest to provision offspring to the floral resource composition of different habitat types in the surrounding landscape. They concluded that these solitary bees will switch foraging behaviors to resources available at organic farms when semi-natural habitats are more distant.

No differences were found in this study between social and solitary bee abundance in contrasts of the two modalities, but large social species were more abundant than solitary ground- and wood-nesters in CRP and pasture, and more abundant than solitary wood-nesters and small social species in prairie. Therefore, a combination of trait modalities within sociality, nesting strategy, floral specificity, and body size appear to influence wild bee distribution in the Southeast Prairies. Due to differences in how

suites of species perceive the surrounding landscape (Roulston and Goodell 2011), social, long-distance foragers may be better able to exploit resources among complementary habitats in this landscape.

A nested composition pattern, with subsets of species within different habitat types, would be expected where environmental filters differentially influence species by functional traits (Aizen et al. 2012; Sasaki et al. 2012). It is typical, however, for species abundances to be uneven within a community, with a few species being dominant and the majority being uncommon or rare (Volkov et al. 2003). In terms of functional composition, most bees are solitary ground-nesters, fewer (about 30%) are wood- or twig-nesters, approximately one quarter are cleptoparasites or social parasites, and oligoleges are less common than polyleges (Mader et al. 2011). Therefore, the community structure of the Southeast Prairies collectively seems to represent a typical healthy assemblage of species, but one that favors large social species with great foraging capacity. One of these species in particular, *Bombus pensylvanicus*, is significant because it is a dominant species in this landscape but has elsewhere so declined in range, persistence, and abundance to be listed as “vulnerable” on the IUCN Red List of Threatened Species and is nearly qualified for “endangered” status (Hatfield et al. 2015). Its dominance in the Southeast Prairies is encouraging as it potentially indicates sufficiently high-quality habitat to sustain a reservoir of this and other pollinator species. Such evidence supports continued efforts to maintain the connectivity and quality of this landscape for conservation of wildlife and ecosystem services.

Initially, the absence of social parasitic species was curious considering the abundance of large social species. However, the nature of social parasites is to hijack an established nest of the host bumble bee species which it mimics, replace the queen as the egg-laying female, and use the existing workers to rear its offspring (Mader et al. 2011). Although the presence of social parasites cannot be confirmed in this study due to the trapping method and this behavior, cleptoparasites of solitary species were collected and indicate a community of wild bees that is robust enough to support parasites.

Whilst the presence of parasites is considered an indication of a healthy community (Sheffield et al. 2013), the absence of specialists is often indicative of deterioration in plant-pollinator networks (Aizen et al. 2012). Specialists and rare species are typically most vulnerable to local extinction (Davies et al. 2004) and it is the links in which they are involved that are first lost within a pollination web. Large body size and solitary behavior are also particularly susceptible to land-use intensification while small size, social behavior, and polylecty have been associated with tolerance of marginal habitat (Rader et al. 2014). In this study, pollen specialists were collected from all habitat types but four of the eight species which were indicative of CRP habitats were oligolectic species, preferring sunflower (*Helianthus* spp.) and other Asteraceae. *Apis mellifera* and *Halictus ligatus*, in contrast, follow the prediction of Rader et al. (2014). Each is a small (relative to *Bombus* spp.), social, polylectic species which appears to perform well in less florally diverse habitat. Other work has demonstrated the flexibility in the foraging activity of bumble bees in response to the availability of high-quality forage, emphasizing specifically that floral diversity is more important than floral density and indicating these

large social bees as essential providers of pollination services (Jha and Kremen 2013). It appears that these bees behave similarly in the Southeast Prairies landscape.

Evaluating community structure using functional traits is an important component of conservation efforts because of patterns of extinction order, but the argument has been made that conserving a few common generalist species is sufficient to sustain ecosystem function (see Schwartz et al. 2000). This could be argued as a valid strategy in the Southeast Prairies given the abundance and apparent importance of large social species to carrying out pollination services. However, since most species in typical communities occur at low abundances (Rabinowitz et al. 1986; Howe 1999), the cumulative role of rare species significantly contributes to ecosystem functioning (Lyons and Schwartz 2001; Lyons et al. 2005). This is also likely important in the context of the Southeast Prairies because of the equitable distribution of functional traits among these grasslands, but it may contribute to pollination services by mechanisms simply unseen in this study.

Conclusions

The results of this study suggest complementary habitat use among grasslands by wild bees with foraging activity driven by floral resource availability and quality. All three habitat types examined here exhibit a rich assemblage and support species from all functional guilds. Therefore, pollination services are offered by a diverse assemblage of bees and are likely strong in the Southeast Prairies because of delivery by suites of species with diverse behaviors. Large social species may be predominant in this function in this landscape, which supports at least one species, *Bombus pensylvanicus*, that is declining elsewhere in its range to the point of vulnerability. Its abundance in the

Southeast Prairies may be evidence that this landscape can serve not only as a reservoir of wild bees and other pollinators for tallgrass prairie ecosystems but also as a reference of potential wild bee diversity to which other studies can be compared when evaluating the vulnerability of fragmented tallgrass prairie landscapes and pollination services in different contexts. It also justifies continued conservation efforts in this landscape to maintain the natural and semi-natural habitats that support this bee community to ensure continued provisioning of services. A trait-based approach which incorporated pollen analysis as a proxy of resource utilization was useful in this study because it helped identify which guilds and in which habitat types bees carry out the bulk of pollination services among these grasslands. Future work may build upon this by identifying whether functional compensation or replacement occurs in other contexts where whole suites of species and entire guilds have declined.

Table 3.1. Variables of functional composition used to characterize the wild bee assemblages of the Southeast Prairies Biologically Unique Landscape into functional guilds. The 5 traits and 23 modalities used to group species into guilds are listed. "Traits" include maximum body size, foraging capacity, nesting behavior (including nest location), breeding strategy, and floral specificity.

Trait	Body size (mm)	Foraging capacity	Nesting strategy†	Breeding strategy‡	Floral specificity
Modality	≤ 8	0-250 m	Ground (+below)	Cleptoparasite (W, G)	Oligolectic
	9-12	250-400 m	Wood, twig (+above)	Social (large)	Polylectic
	13-16	400-800 m	Cavity (above/below)	Social (small)	
	17-20	800-1200 m	None (parasite)	Gregarious	
	21-27	>1200 m		Solitary	

Notes: Traits were assigned after viewing the range of traits that the collected species exhibit, traits are natural history characteristics, biological characteristics, behavioral characteristics, and physiological characteristics. The trait profiles and guild assignments for each species are provided in Appendix G.

†Nesting strategy and nest location traits are listed together, with nest location (above or below ground) given in parentheses. Cavity nesters can be either, with some species living in abandoned rodent burrows in the ground, others in hollow tree cavities, or in grass hummocks above ground.

‡Cleptoparasitic species are further categorized as parasites of wood- or ground-nesting species (W or G, respectively). No social parasites were collected so only cuckoo bees that parasitize solitary species were included.

Table 3.2. Results of one-way analysis of variance and Holm-Sidak multiple comparisons on wild bee species richness, abundance, evenness, and diversity indices for three grassland habitat types of the Southeast Prairies Biologically Unique Landscape. Means are given for CRP (C), grazed pasture (G), and remnant prairie sites (R), ± 1 SE. *F*-statistics and *P* values of ANOVAs are given, with significance indicated with boldface type. *P* values are also listed for Holm-Sidak contrasts between habitat types (CRP—CRP, PAS—grazed pasture, and PRA—remnant prairie with an overall significance level of 0.05).

ANOVA factor or Holm-Sidak contrast	Bee species richness	Bee species abundance	Evenness (H/H_{\max})	Shannon entropy (H)	Effective species $\text{Exp}(H)$	Gini-Simpson index (D')
Means						
	C: 39.80 \pm 2.059	C: 614.6 \pm 100.6	C: 0.781 \pm 0.012	C: 2.872 \pm 0.048	C: 17.75 \pm 0.806	C: 0.913 \pm
	G: 36.00 \pm 1.225	G: 410.8 \pm 83.24	G: 0.785 \pm 0.020	G: 2.809 \pm 0.057	G: 16.71 \pm 0.929	0.002
	R: 38.60 \pm 2.379	R: 577.8 \pm 46.93	R: 0.729 \pm 0.012	R: 2.653 \pm 0.027	R: 14.22 \pm 0.388	G: 0.911 \pm
						0.007
						R: 0.887 \pm
						0.004
ANOVA results						
<i>F</i> -statistic	2,12	1.838	4.287	5.991	5.930	8.091
<i>p</i> -value	0.993	0.201	0.039	0.016	0.016	0.006
Holm-Sidak contrasts						
1) CRP—PAS	0.671	0.264	0.842	0.357	0.344	0.726
2) CRP—PRA	0.475	0.751	0.063	0.017	0.017	0.010
3) PAS—PRA	0.596	0.305	0.064	0.066	0.070	0.013

Notes: Shannon entropy (H) is the Shannon-Weiner diversity index. Bee community evenness is measured as H/H_{\max} , where $H_{\max} = \ln(\text{species richness})$. Effective species is the exponential of Shannon entropy.

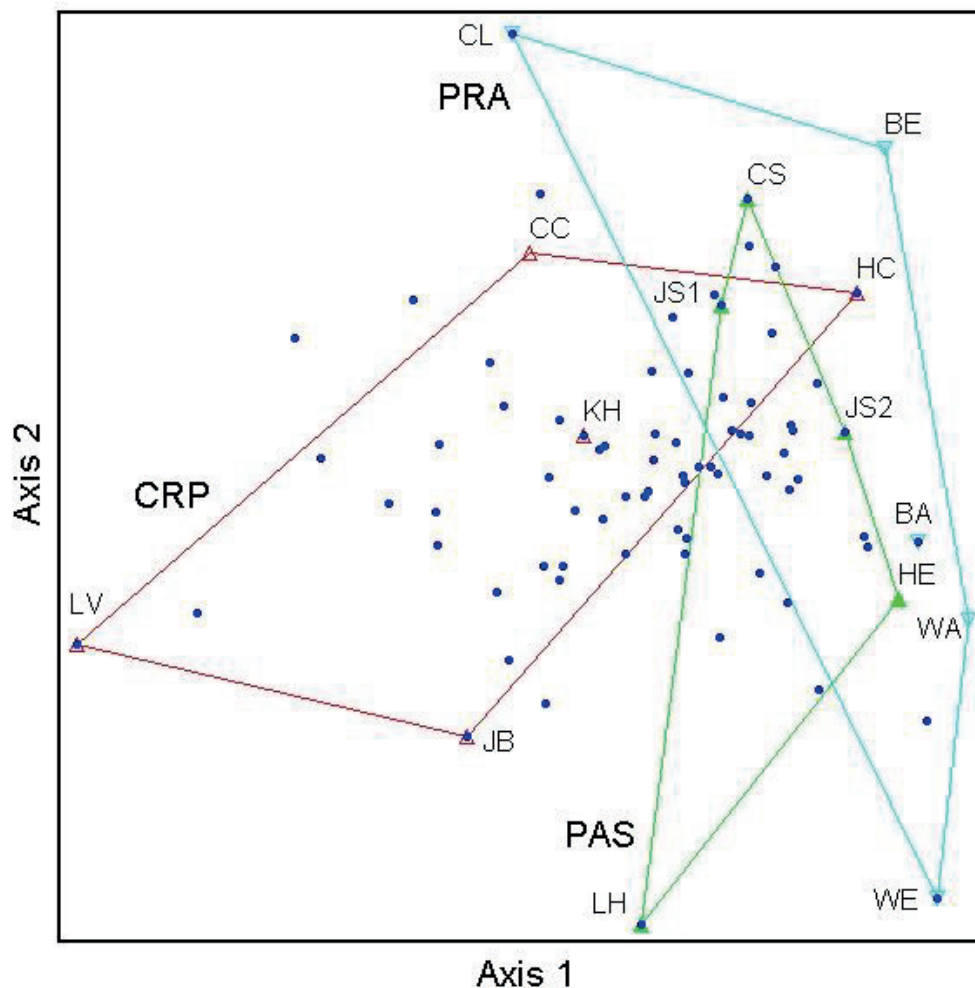


Figure 3.1. Nonmetric multidimensional scaling ordination of wild bee communities from three habitat types in the Southeast Prairies Biologically Unique Landscape. The ordination is a two-dimensional solution that explains 84.7% of variation, 61.7 on axis 1, and 23.0% on axis 2. CRP sites are outlined in red, grazed pasture (PAS) in green, and remnant prairie sites (PRA) are outlined in blue. Dark blue dots represent wild bee species plotted by relative Sørensen dissimilarities.

Table 3.3. Differences in the composition of bee species assemblages between three grassland types in the Southeast Prairies Biologically Unique Landscape. Results of multiple response permutation procedures on blooming forb species from CRP, grazed pasture (PAS), and remnant prairie (PRA) habitats using abundance (*Ab*) and presence-absence (*P/A*) data are listed. Within-group agreement (*A*), and probability of an equal or smaller delta (*p*) are shown. Significant differences among groups are indicated in bold with an overall significance level of 0.05.

Within-Group Agreement & Multiple Comparisons	Within-Group Agreement (<i>A</i>)	Probability of \leq Delta (<i>p</i>)
Overall (<i>Ab</i>)	0.012	0.287
Overall (<i>P/A</i>)	0.003	0.406
Multiple Comparisons (<i>Ab</i>)		
1) CRP—PAS	0.006	0.346
2) CRP—PRA	0.043	0.077
3) PAS—PRA	-0.025	0.762
Multiple Comparisons (<i>P/A</i>)		
1) CRP—PAS	0.018	0.230
2) CRP—PRA	-0.007	0.516
3) PAS—PRA	-0.003	0.496

Notes: MRPP tests the hypothesis of no difference between communities based on among- and within-group dissimilarities. The probability of an equal or lesser delta is determined through Monte Carlo permutations and represents the fraction of 999 permuted deltas that are less than the observed delta.

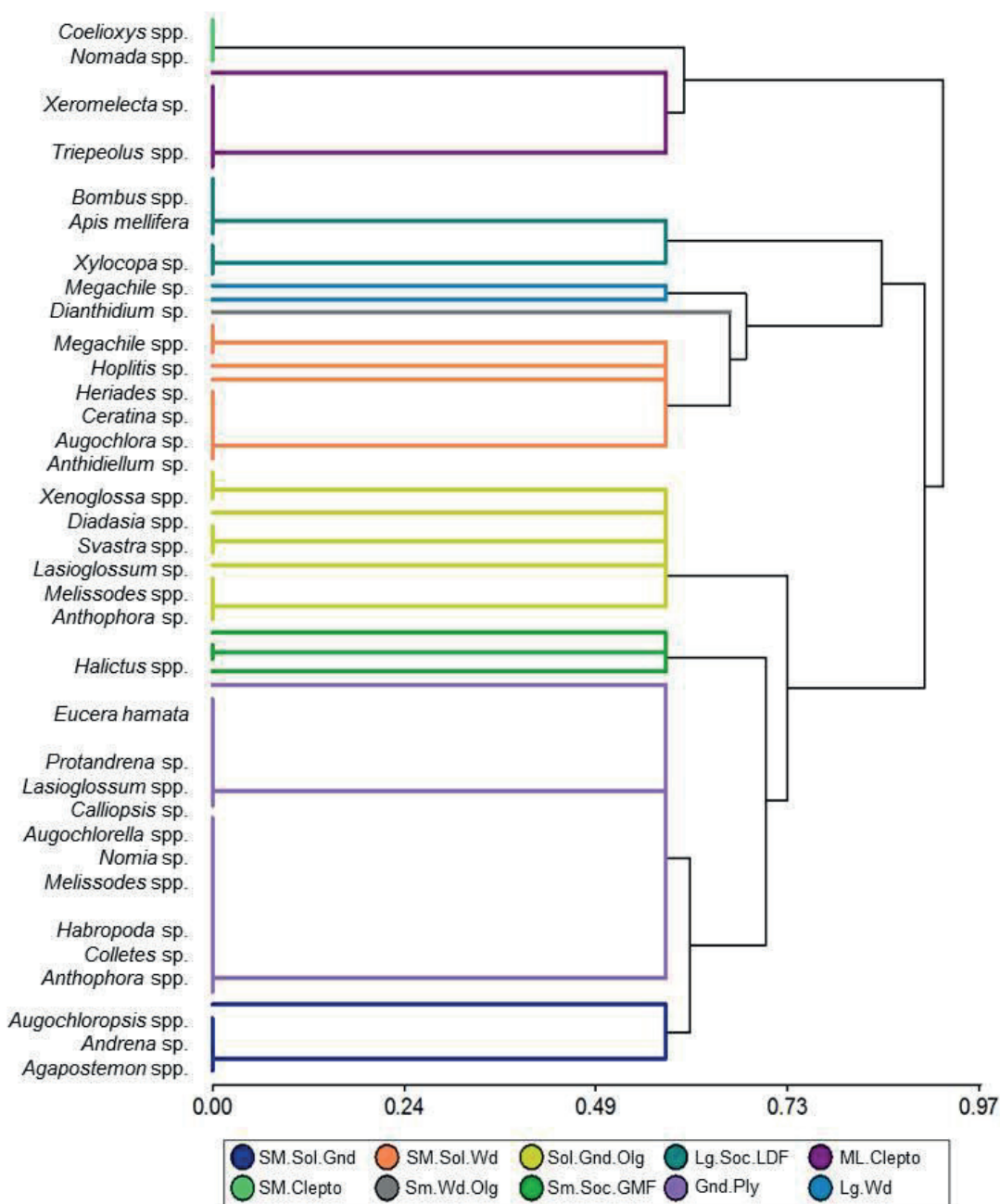


Figure 3.2. Results of cluster analysis on bee species using trait modalities to categorize species into functional guilds. Genera are listed to the left of the dendrogram and functional guilds are color-coded in the key. Clusters are based Jaccard distances ($\sqrt{1-S}$) between species calculated from trait profiles, which consisted of binary data for each modality. Average linkage was the linkage algorithm and the cophenetic correlation was 0.970 based on 601 cases of species occurrences within 15 study sites. (See Table 3.4 for descriptions of functional guilds).

Table 3.4. Functional guilds of wild bees resulting from cluster analysis of species' modalities within five traits. The number of species and proportion of individuals assigned to each of ten functional guilds are listed. Cluster analysis was performed on the trait profile of each species using average linkage as the linkage algorithm and the Jaccard method for a distance matrix to categorize species from 15 study sites into the 10 functional guilds described here.

Functional guild	Description	No. species	Proportion
Gnd.Ply (GP)	Ground-nesting generalists (polylectic ground-nesters, varying sizes and foraging capacities)	24	0.396
Lg.Soc.LDF (LS)	Large, social, long-distance foragers (eusocial cavity-nesters (bumble bees and honey bees))	8	0.182
Lg.Wd (LW)	Large, wood-nesting excavators	2	0.072
ML.Clepto (MC)	Cleptoparasites of medium-large, ground-nesting solitary bees	8	0.003
SM.Clepto† (SC)	Cleptoparasites of small-medium, wood-nesting solitary bees	4	0.002
Sm.Soc.GMF (SS)	Small social, ground-nesting bees with moderate foraging capacity (social Halictids)	4	0.054
SM.Sol.Gnd‡ (SG)	Medium, solitary ground-nesting sweat bees (solitary Halictids)	5	0.175
SM.Sol.Wd (SW)	Small-medium, solitary wood-nesting excavators	11	0.021
Sm.Wd.Olg (WO)	Small, oligolectic wood-nesting excavators	1	0.001
Sol.Gnd.Olg (GO)	Solitary oligolectic ground-nesting excavators	12	0.094

Notes: † *Coelioxys* spp. are parasites of *Megachile* spp. while *Nomada* spp. are often parasites of *Andrena* spp., but both comprise "SM.Clepto."

‡ All species clustered in "SM.Sol.Gnd" are medium-size sweat bees (Halictidae) except for *Andrena cressonii* (Andrenidae).

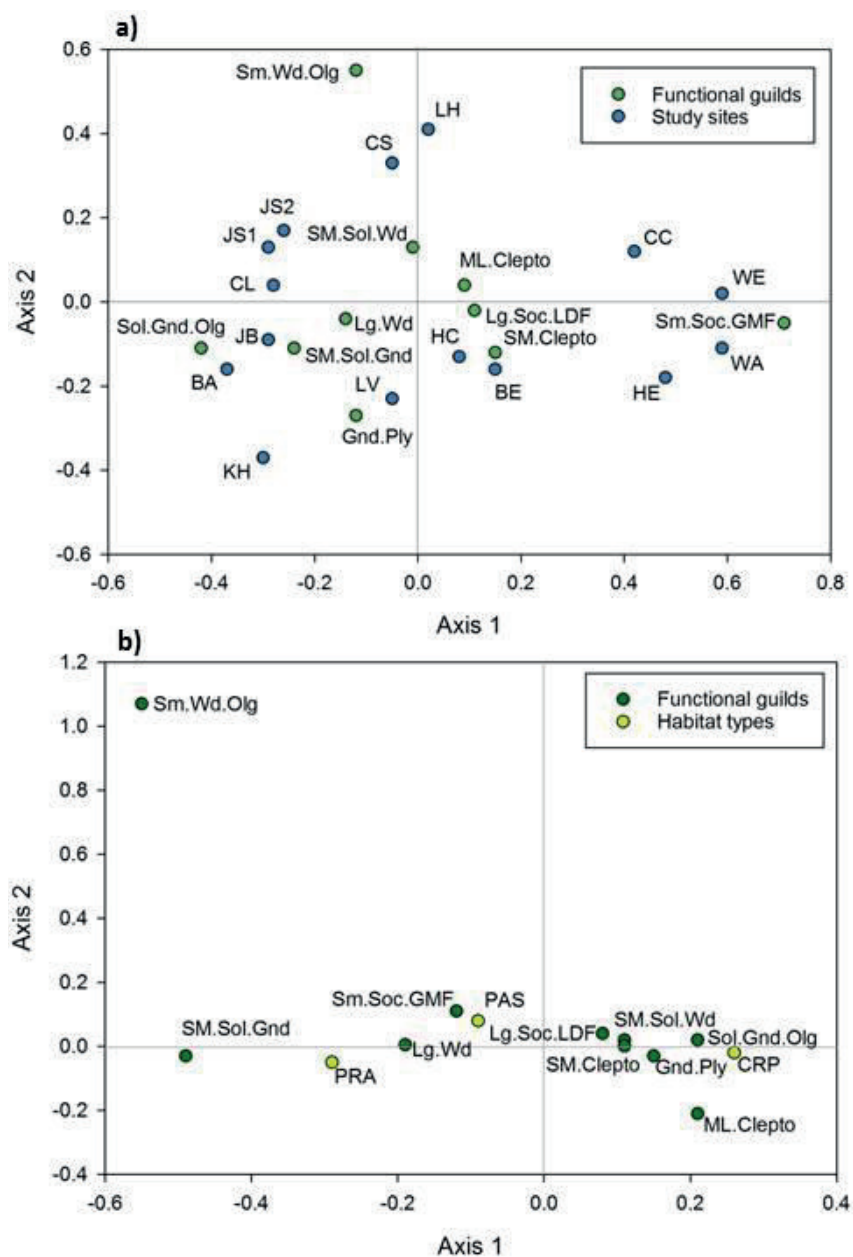


Figure 3.3. Biplots of correspondence analyses used to explore the potential associations of bee functional guilds with a) study sites and b) habitat types in the Southeast Prairies Biologically Unique Landscape. The two axes of functional guilds and study sites explain 74.2% of variability (53.38% on axis 1, 20.82% on axis 2) and the axes for functional guilds and habitat type explain 100% of variability (95.44% on axis 1 and 4.56% on axis 2).

Table 3.5. Results of one-way Analysis of Variance or Kruskal-Wallis H tests for ten functional guilds of wild bees collected from three habitat types in the Southeast Prairies Biologically Unique Landscape. Means are given for CRP, grazed pasture (PAS), and remnant prairie sites (PRA), ± 1 SE for ground-nesting generalists (GP), large social bees (LS), large wood-nesters (LW), medium (MC) and small (SC) cleptoparasites, small social bees (SS), small ground-nesters (SG), small wood-nesters (SW), and wood- (WO) and ground-nesting (GO) oligoleges. The numbers listed from ANOVA represent *F*-statistic or *H*-score and *P* values. Bold face highlights significant factors. *P* values are also listed for Holm-Sidak or Tukey contrasts between habitat types (CRP—CRP, PAS—grazed pasture, and PRA—remnant prairie with an overall significance level of 0.05).

Habitat means, ANOVA factor or contrast	GP	LS	LW	MC	SC	SS	SG	SW	WO	GO
Means	294.2 (46.02)	119.4 (37.56)	35.20 (8.145)	2.20 (1.02)	1.20 (0.735)	27.80 (4.017)	46.00 (12.71)	15.60 (3.614)	0.00 (0.00)	73.00 (18.04)
PAS	142.4 (22.47)	81.20 (18.04)	30.40 (5.124)	0.60 (0.40)	0.60 (0.40)	26.60 (6.809)	84.40 (39.59)	8.00 (1.378)	1.00 (0.447)	35.60 (14.46)
PRA	198.0 (52.94)	91.80 (15.46)	49.60 (16.38)	1.60 (0.678)	1.00 (0.632)	32.40 (4.094)	150.6 (36.28)	10.20 (0.97)	0.40 (0.40)	42.20 (10.97)
ANOVA results (df)										
<i>F</i> -statistic (2,12)	3.262	0.591	0.830	1.181	—	0.355	2.758	—	—	—
<i>H</i> -score (2)	—	—	—	—	0.380	—	—	2.830	4.133	4.170
<i>p</i> -value	0.074	0.569	0.460	0.340	0.779	0.708	0.103	0.095	0.127	0.124
Holm-Sidak or Tukey contrasts										
CRP-PAS	0.078	0.676	0.762	0.395	0.873	0.872	0.411	0.109	0.180	0.268
CRP-PRA	0.253	0.710	0.605	0.579	0.819	0.787	0.112	0.231	0.430	0.305
PRA-PAS	0.373	0.775	0.560	0.591	0.877	0.825	0.307	0.512	0.429	0.758

Table 3.6. Results of Kruskal-Wallis H test on functional guilds of CRP, grazed pasture, and remnant prairie habitats of the Southeast Prairies Biologically Unique Landscape. Contrasts are given for ground-nesting generalists (GP, GndPly), large social long-distance foragers (LS, Lg.Soc.LDF), large wood-nesters (LW, Lg.Wd), medium (MC, ML.Clepto) and small (SC, SM.Clepto) cleptoparasites, small social species ground-nesters (SS, Sm.Soc.GMF), solitary sweat bees (SG, SM.Sol.Gnd), small solitary wood-nesters (SW, SM.Sol.Wd), and wood (WO, SM.Wd.Olg) and ground-nesting (GO, Sol.Gnd.Olg) oligoleges ± 1 SE. Bold face highlights significant differences between guilds at an overall significance level of 0.05. Boldface highlights significant differences between guilds within each habitat. Significant contrasts in Tukey tests with an overall significance level of 0.05 are indicated by noting the guilds with lower abundance.

ANOVA factor or contrast		CRP	Grazed Pasture	Remnant Prairie
Means		See Table 3.5 for guild means ± 1 S.E. within each habitat type.		
ANOVA results	df			
<i>H</i> -score	9	44.171	43.329	44.154
<i>p</i> -value		< 0.001	< 0.001	< 0.001
Tukey contrasts				
1) Gnd.Ply		WO, SC, MC	SC, MC, WO	WO, SC, MC
2) Lg.Soc.LDF		WO, SC, MC	SC, MC, WO	WO, SC
3) Lg.Wd		none	none	none
4) ML.Clepto		none	none	none
5) SM.Clepto		none	none	none
6) Sm.Soc.GMF		none	none	none
7) SM.Sol.Gnd		none	SC, MC	WO, SC, MC
8) SM.Sol.Wd		none	none	none
9) SM.Wd.Olg		none	none	none
10) Sol.Gnd.Olg		WO	none	none

Notes: Means are given for each of the 10 functional guilds within each habitat type ± 1 S.E in the previous table (Table 3.5).

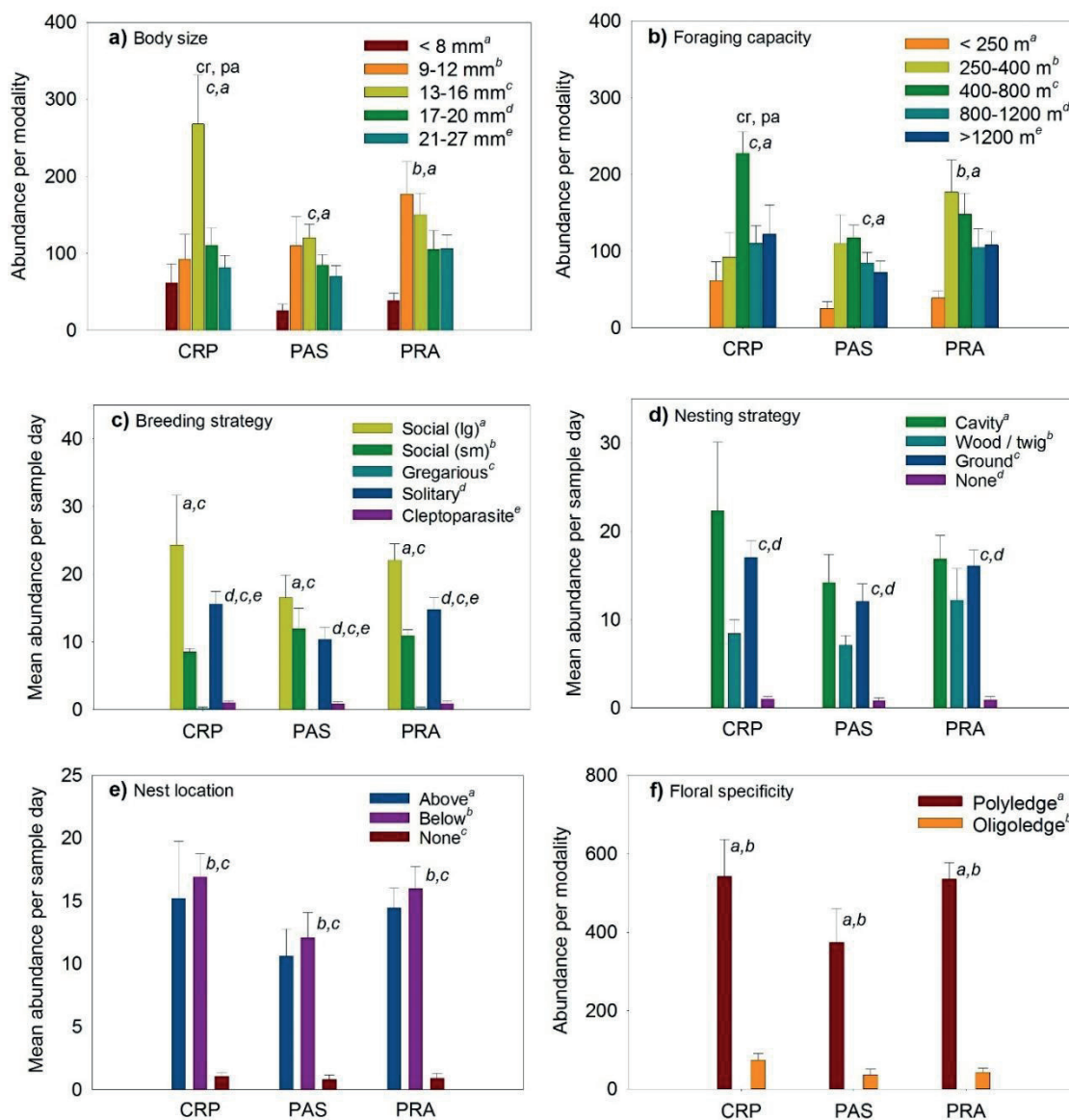


Figure 3.4. Distribution of abundance-weighted modalities for six traits of wild bees from three habitat types in the Southeast Prairies BUL: a) maximum body size, b) foraging capacity, c) breeding strategy, d) nesting strategy, e) nest location, and f) floral specificity from within conservation reserve program (CRP), grazed pasture (PAS) and remnant prairie (PRA). Lower case letters indicate a significant difference in the distribution of a modality either between or within habitat types (CRP—cr, grazed pasture—pa, and remnant prairie—pr; $p < 0.05$) in one-way ANOVA with Holm-Sidak contrast.

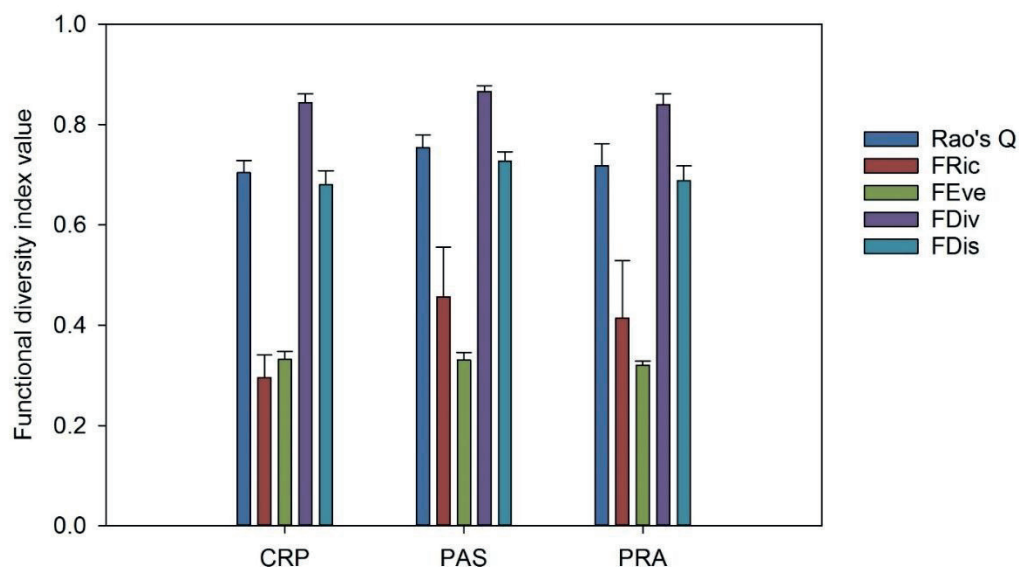


Figure 3.5. Functional diversity indices of wild bee assemblages from three habitat types in the Southeast Prairies Biologically Unique Landscape. Plotted are a) Rao's quadratic entropy (F_Q), relative to maximum for CRP, grazed pasture (PAS) and remnant prairie (PRA), and functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis) for b) CRP, c) grazed pasture, and d) remnant prairie. Boxplots represent functional diversity index value means and variance for five study sites within each habitat type. No significant differences between habitat types were found for any indices or components of functional diversity (ANOVA with Holm-Sidak or Kruskal-Wallis H test with Tukey test of multiple comparisons ($p < 0.05$)) and, therefore, none are indicated.

Table 3.7. Results of one-way ANOVA with Holm-Sidak contrasts and Kruskal-Wallis H test with Tukey contrasts on the blooming forb communities of three grassland habitat types of the Southeast Prairies Biologically Unique Landscape. Means are given for CRP (C), grazed pasture (G), and remnant prairie sites (R), ± 1 SE. The numbers listed from ANOVA represent *F*-statistic or *H*-score and *P* values. *P* values are also listed for Holm-Sidak or Tukey contrasts between habitat types (CRP—CRP, PAS—grazed pasture, and PRA—remnant prairie. Boldface highlights significant factors and contrasts with an overall significance level of 0.05.

ANOVA factor, Holm-Sidak or Tukey contrast		Forb species		Forb abundance	Evenness (H/H_{\max})	Shannon entropy (<i>H</i>)	Gini-Simpson index (<i>D'</i>)
Means		C: 14.80 \pm 2.596	C: 3470.4 \pm 2259.7	C: 0.479 \pm 0.080	C: 1.310 \pm 0.269	C: 0.581 \pm 0.117	
		G: 17.40 \pm 2.379	G: 1256.6 \pm 504.59	G: 0.651 \pm 0.046	G: 1.813 \pm 0.091	G: 0.767 \pm 0.028	
		R: 27.40 \pm 1.691	R: 8921.6 \pm 905.01	R: 0.543 \pm 0.036	R: 1.792 \pm 0.117	R: 0.720 \pm 0.047	
ANOVA results		df					
<i>F</i> -statistic	2,12	8.700	--	2.347	2.577	--	
<i>H</i> -score	2	--	6.500	--	--	2.880	
<i>p</i> -value		0.005	0.039	0.138	0.117	0.237	
Holm-Sidak or Tukey contrasts							
1) CRP—PAS		0.431	0.759	0.151	0.190	0.206	
2) CRP—PRA		0.006	0.181	0.438	0.151	0.673	
3) PAS—PRA		0.017	0.036	0.367	0.935	0.673	

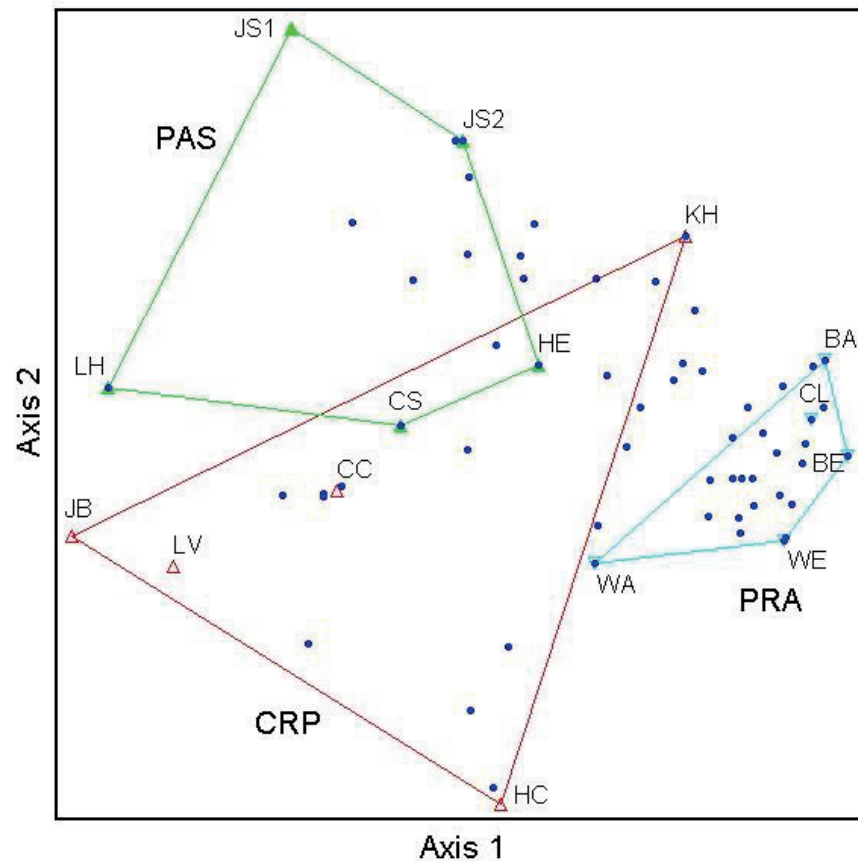


Figure 3.6. Nonmetric multidimensional scaling ordination of blooming forb species and study sites from three habitat types in the Southeast Prairies BUL. The ordination has a two-dimensional solution that explains 76.7% of variation (35.7% and 41%) with a final stress of 14.14 and final instability of 0.00, based on 56 iterations. Red symbols and connecting lines represent CRP study sites. Green indicates grazed pasture (PAS). Blue indicates remnant prairie (PRA). The blue dots represent species of blooming forbs observed at the time that bees were collected from study sites.

Table 3.8. Differences in the composition of blooming forbs between three grassland types in the Southeast Prairies Biologically Unique Landscape. Results of multiple response permutation procedures on blooming forb species from CRP, grazed pasture (PAS), and remnant prairie (PRA) habitats using abundance (*Ab*) and presence-absence (*P/A*) data are listed. Within-group agreement (*A*), and probability of an equal or smaller delta (*p*) are shown. Significant differences among groups are indicated in bold with an overall significance level of 0.05.

Community Comparisons	Within-Group Agreement (<i>A</i>)	Probability of \leq Delta (<i>p</i>)
Overall (<i>Ab</i>)	0.145	0.0006
Overall (<i>P/A</i>)	0.176	< 0.0001
Multiple Comparisons (<i>Ab</i>)		
4) CRP—PAS	0.033	0.101
5) CRP—PRA	0.155	0.007
6) PAS—PRA	0.167	0.004
Multiple Comparisons (<i>P/A</i>)		
4) CRP—PAS	0.031	0.092
5) CRP—PRA	0.218	0.001
6) PAS—PRA	0.176	0.001

Notes: MRPP tests the hypothesis of no difference between communities based on among- and within-group dissimilarities. The probability of an equal or lesser delta is determined through Monte Carlo permutations and represents the fraction of 999 permuted deltas that are less than the observed delta.

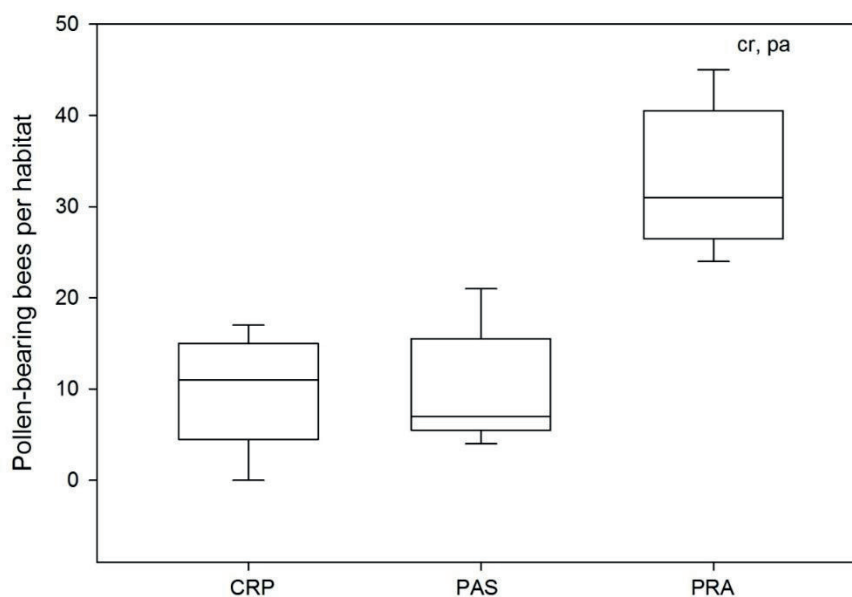


Figure 3.7. Number of pollen-bearing bees from within each of three habitat types (CRP, grazed pasture (PAS) and remnant prairie (PRA)) within the Southeast Prairies BUL are plotted \pm S.E. Significant differences from Holm-Sidak tests of multiple comparisons following one-way ANOVA on means of the number of pollen-bearing bees are indicated with lower case initials: CRP—cr, grazed pasture—pa, remnant prairie—pr.

Table 3.9. Pollen-bearing bees of the Southeast Prairies Biologically Unique Landscape. Listed for each species is the abundance within CRP, grazed pasture (PAS), and remnant prairie (PRA) sites, as well as the overall total in the Southeast Prairies BUL and the relative percent of pollen bearing bees.

Species	CRP	PAS	PRA	Total (Rel. %)
<i>Bombus pensylvanicus</i>	0	7	16	93 (35.2%)
<i>Bombus auricomus</i>	1	0	0	59 (22.3%)
<i>Eucera hamata</i>	0	0	1	55 (20.8%)
<i>Agapostemon virescens</i>	10	14	35	23 (8.7%)
<i>Xylocopa virginica</i>	0	2	2	10 (3.8%)
<i>Megachile montevega</i>	0	1	0	9 (3.4%)
<i>Bombus bimaculatus</i>	20	17	56	4 (1.5%)
<i>Halictus parallelus</i>	10	0	45	4 (1.5%)
<i>Apis mellifera</i>	1	0	3	1 (0.38%)
<i>Augochlorella aurata</i>	0	0	1	1 (0.38%)
<i>Bombus griseocollis</i>	1	0	0	1 (0.38%)
<i>Halictus rubicundus</i>	0	0	1	1 (0.38%)
<i>Lasioglossum v. callidum</i>	0	0	1	1 (0.38%)
<i>Melissodes bimaculata</i>	2	4	3	1 (0.38%)
<i>Melissodes comptoides</i>	5	4	1	1 (0.38%)
Total of pollen-bearing bees	50	49	165	264

Notes: A total of 264 pollen-bearing bees were collected, comprising, or 3.3% of the 8,016 individuals considered in the Southeast Prairies BUL assessment.

Table 3.10. Results of Kruskal-Wallis H test on the number of pollen-bearing bees within functional guilds of CRP, grazed pasture, and remnant prairie habitats of the Southeast Prairies Biologically Unique Landscape. Means are given for ground-nesting generalists (GP, GndPly), large social long-distance foragers (LS, Lg.Soc.LDF), large wood-nesters (LW, Lg.Wd), small social species ground-nesters (SS, Sm.Soc.GMF), solitary sweat bees (SG, SM.Sol.Gnd), and solitary wood-nesters (SW, SM.Sol.Wd) \pm 1 SE. Bold face highlights significant differences between guilds at an overall significance level of 0.05.

ANOVA factor or contrast		CRP	Grazed Pasture	Remnant Prairie
Means		GP: 2.20 \pm 1.20	GP: 0.00 \pm 0.00	GP: 9.60 \pm 2.54
		LS: 6.20 \pm 2.22	LS: 6.80 \pm 1.59	LS: 18.6 \pm 4.09
		LW: 1.00 \pm 0.78	LW: 0.80 \pm 0.80	LW: 0.20 \pm 0.20
		SS: 0.20 \pm 0.20	SS: 0.00 \pm 0.00	SS: 0.80 \pm 0.49
		SG: 0.00 \pm 0.00	SG: 1.40 \pm 1.17	SG: 3.20 \pm 1.28
		SW: 0.40 \pm 0.24	SW: 0.80 \pm 0.80	SW: 0.60 \pm 0.60
ANOVA results				
	df			
<i>H</i> -score	4	11.227	18.100	19.172
<i>p</i> -value		0.047	0.003	0.002
Tukey contrasts				
1) Gnd.Ply		none	--	none
2) Lg.Soc.LDF		GP, SW, LW	SW, LW, SG	LW, SW, SS
3) Lg.Wd		none	none	none
4) Sm.Soc.GMF		--	none	none
5) SM.Sol.Gnd		none	--	none
6) SM.Sol.Wd		none	none	none

Notes: Significant contrasts in Tukey tests with an overall significance level of 0.05 are indicated by noting the guilds with fewer pollen-bearing bees. Functional guilds with no pollen-bearing bees in any habitat were excluded.

Table 3.11. Community similarity for wild bees and blooming forbs from three grassland habitat types in the Southeast Prairies Biologically Unique Landscape. Listed are the number of bee species, functional guilds, and traits shared between CRP, grazed pasture (PAS) and remnant prairie (PRA) habitats, as well as the number of shared forb species and pollen types. These are accompanied by mean Sørensen similarity indices, with standard errors given in parentheses.

Community measurement	Shared species*			Sørensen similarity		
	CRP-PAS	CRP-PRA	PAS-PRA	CRP-PAS	CRP-PRA	PAS-PRA
Bee species	50	55	60	0.75 (0.01)	0.75 (0.01)	0.77 (0.01)
Functional guilds	9	9	10	0.90 (0.02)	0.93 (0.02)	0.91 (0.01)
Trait modalities	23	24	23	0.96 (0.01)	0.96 (0.01)	0.998 (0.001)
Blooming forbs	25	20	26	0.45 (0.05)	0.34 (0.03)	0.42 (0.03)
Pollen types	11	19	13	0.27 (0.07)	0.27 (0.03)	0.22 (0.04)

Notes: Sørensen similarity values = $1 - \text{Sørensen distance}$ based on five study sites from each habitat type. Listed are the means of comparisons between each of the study sites from each of the habitat types within a given pair of habitat comparisons.

*For shared species, “species” indicates the number of shared species, guilds, modalities, or pollen types.

Table 3.12. Association between the wild bee and blooming forb communities in the Southeast Prairies Biologically Unique Landscape. Results of Mantel tests of association between the bee community and floral resource availability are given as standardized Mantel statistics (r). The nature of association (+/-), and p -values are also listed for bee species, functional guilds, and trait modalities compared with blooming forb species and pollen types. Significant associations were those with $P \leq 0.05$.

Communities tested for association	Mantel statistic (r)	Association	Significance
Bee species—blooming forbs	0.033	none (+)	0.375
Functional guilds—blooming forbs	-0.063	none (-)	0.261
Trait modalities—blooming forbs	-0.033	none (-)	0.400
Pollen-bearing bees—blooming forbs	0.203	none (+)	0.061
Pollen-bearing guilds—blooming forbs	0.073	none (+)	0.264
Bee species—pollen types	-0.191	none (-)	0.363
Functional guilds—pollen types	-0.180	none (-)	0.286
Pollen-bearing bees—pollen types	-0.121	none (-)	0.354
Pollen-bearing guilds—pollen types	-0.104	none (-)	0.379
Blooming forbs—pollen types	0.017	none (+)	0.455

Notes: Mantel tests used relative Sorensen distances for each community measure based on 999 randomized runs to test the null hypothesis that there is no relationship between community matrices. Positive associations were indicated by observed Z (sum of cross products) larger than average Z of these randomized runs. P -values represent the proportion of randomized runs with Z more extreme than or equal to the observed Z .

Table 3.13. Correlations of floral resources to the wild bee community of the Southeast Prairies Biologically Unique Landscape. Correlation coefficients and p -values of Pearson product moment (black) and Spearman rank (blue) correlations are listed. Significant correlations, with a significance level of 0.05, are indicated with boldface. Diversity measures include Shannon diversity (H), community evenness (H/H_{max}) and Simpson's dominance (D). Functional diversity measures of wild bees include Rao's quadratic entropy (F_Q), functional richness (FRic), evenness (FEve), divergence (FDiv), and dispersion (FDis). Correlations within pollen-bearing bees were also considered.

Measurement of bee	Blooming forbs					
	Abundance	Density	Species richness	Evenness	H	D
Bee species diversity measurements						
Abundance	0.668	0.525	0.418	-0.171	-0.254	-0.179
	0.0065	0.0429	0.121	0.541	0.353	0.514
Species richness	0.396	0.517	0.272	-0.189	-0.326	-0.3
	0.144	0.0463	0.327	0.5	0.23	0.269
Evenness	-0.602	-0.517	-0.698	-0.0012	-0.084	-0.025
	0.0175	0.0463	0.0038	0.997	0.753	0.923
H	-0.423	-0.257	-0.613	-0.119	-0.35	-0.279
	0.117	0.346	0.015	0.673	0.194	0.306
D'	-0.547	-0.439	-0.681	0.0512	-0.154	-0.0643
	0.0348	0.0975	0.0052	0.856	0.575	0.812
Functional diversity measurements						
F_Q	0.102	-0.0987	0.117	0.268	0.117	0.122
	0.718	0.714	0.678	0.334	0.667	0.657
FRic	-0.085	-0.085	0.221	0.329	0.536	0.447
	0.753	0.753	0.418	0.224	0.0382	0.0917

Table 3.13 (continued).

Measure of bee diversity	Blooming forbs					
	Abundance	Density	Species richness	Evenness	H	D'
FEve	-0.277	-0.281	-0.411	-0.0223	-0.121	-0.0685
	0.317	0.3	0.128	0.937	0.657	0.802
FDiv	0.00162	-0.128	-0.0905	0.361	0.0811	0.0901
	0.995	0.639	0.748	0.187	0.763	0.743
FDis	0.0255	-0.132	0.00328	0.303	0.0393	0.075
	0.928	0.629	0.991	0.272	0.883	0.783
<i>Pollen-bearing bees</i>						
Number	0.690	0.777	0.798	0.0324	0.275	0.129
	0.0044	< 0.0001	0.0004	0.909	0.312	0.639
Proportion	0.625	0.625	0.888	0.071	0.511	0.329
	0.0123	0.0123	< 0.0001	0.793	0.0498	0.224

Notes: Spearman rank correlation analyses were performed when variables failed Shapiro-Wilk tests of normality and are indicated in blue. Forb and bee abundance were transformed by natural logarithm to achieve normality. Forb density is the number of blooming stems per square meter. Forb and bee evenness was measured as H/H_{\max} , where $H_{\max} = \ln(\text{species richness})$. Significant linear correlations prior to Bonferroni correction for multiple comparisons are indicated in bold. Following adjustment, only measures where $p \leq 0.0083$ retained significance. Strength of associations follows Cohen (1988): weak— $0.1 < |r| < 0.3$, moderate— $0.3 < |r| < 0.5$, strong— $|r| > 0.5$.

Table 3.14. Results of Monte Carlo test of significance on indicator values for wild bees, functional guilds, and trait modalities within three habitat types in the Southeast Prairies BUL. Listed are the habitat types (remnant prairie, grazed pasture, or CRP) in which a bee species, guild, or trait is significantly abundant and constant, their indicator values (IV), the mean abundance and standard deviation, and the p -value.

Species/Guild/Modality	Habitat (max)	IV	Mean (s.d.)	p -value
Bees				
<i>Anthophora walshii</i>	CRP	62.5	45.5 (6.60)	0.0166
<i>Apis mellifera</i>	CRP	93.0	90.7 (1.70)	0.0236
<i>Diadasia enavata</i>	CRP	60.3	48.5 (5.54)	0.0174
<i>Halictus ligatus</i>	CRP	66.8	45.0 (10.68)	0.0522
<i>Lasioglossum nymphaearum</i>	Prairie	56.8	29.2 (12.92)	0.0416
<i>Melissodes agilis</i>	CRP	57.4	49.3 (6.87)	0.0440
<i>Melissodes bimaculata</i>	CRP	57.3	42.2 (4.86)	0.0058
<i>Melissodes coloradensis</i>	CRP	61.8	39.0 (10.29)	0.0400
<i>Melissodes comptoides</i>	CRP	48.4	40.9 (4.12)	0.0564
Functional Guilds				
Ground-nesting generalists	CRP	41.4	37.3 (2.23)	0.0476
Trait Modalities				
Foraging capacity 400-800m	CRP	46.1	38.8 (3.00)	0.0154
Max. body size 13-16 mm	CRP	49.8	42.2 (3.44)	0.0146

Notes: Habitat (max) indicates the habitat in which the maximum indicator value (IV) was observed. The p -values listed represent the proportion of 4999 randomized trials in a Monte Carlo simulation in which indicator values equal or exceed the observed indicator value. A small p -value indicates that a species is more abundant and constant than would be expected by chance.

Table 3.15. Results of Monte Carlo test of significance on indicator values of blooming forbs and pollen collected from wild bees within three habitat types in the Southeast Prairies BUL. Listed are the habitat types (remnant prairie, grazed pasture, or CRP) in which species or pollen types are significantly abundant and constant, the indicator value (IV) of those species, the mean abundance and standard deviation, and the p -value.

Species	Habitat (max)	IV	Mean (s.d.)	p -value
Blooming Forbs				
<i>Achillea millefolium</i>	Prairie	87.7	43.1 (11.64)	0.0020
<i>Amorpha canescens</i>	Prairie	100.0	31.0 (13.74)	0.0008
<i>Dalea candida</i>	Prairie	90.0	37.9 (14.83)	0.0042
<i>Linum sulcatum</i>	Prairie	100.0	31.0 (13.61)	0.0008
<i>Potentilla recta</i>	Prairie	100.0	30.3 (13.36)	0.0008
<i>Psoraleidum tenuiflorum</i>	Prairie	100.0	33.5 (13.58)	0.0008
<i>Rudbeckia hirta</i>	Prairie	86.2	49.2 (10.17)	0.0008
<i>Silphium laciniatum</i>	Prairie	80.0	27.2 (12.69)	0.0080
<i>Symphotrichum ericoides</i>	Prairie	75.1	38.4 (14.58)	0.0180
<i>Trifolium pratense</i>	Prairie	81.2	48.5 (12.88)	0.0132
<i>Verbena stricta</i>	Pasture	97.8	42.2 (15.80)	0.0008
Pollen Types*				
<i>Achillea millefolium</i>	Prairie	0.734	0.286 (0.146)	0.0046
<i>Amorpha canescens</i>	Prairie	1.000	0.288 (0.156)	0.0006
<i>Ceanothus herbaceus</i>	Prairie	0.877	0.293 (0.156)	0.0064
<i>Dalea candida</i>	Prairie	0.877	0.293 (0.156)	0.0064
<i>Melilotus alba</i>	Pasture	0.853	0.301 (0.156)	0.0050
<i>Potentilla recta</i>	Prairie	1.000	0.288 (0.156)	0.0006

Table 3.15 (continued).

Species	Habitat (max)	IV	Mean (s.d.)	p-value
<i>Psoraleidum tenuiflorum</i>	Prairie	0.853	0.279 (0.165)	0.0030
<i>Symphotrichum ericoides</i>	Prairie	0.756	0.301 (0.156)	0.0148
<i>Verbena stricta</i>	Pasture	0.866	0.289 (0.155)	0.0026

Notes: Habitat (max) indicates the habitat in which the maximum indicator value (IV) was observed. The *p*-values listed represent the proportion of 4999 randomized trials in a Monte Carlo simulation in which indicator values equal or exceed the observed indicator value. A small *p*-value indicates that a species is more abundant (for blooming forbs) and constant than would be expected by chance.

*Pollen types are presence/absence data so indicator values are calculated with Tichy and Chytry (2006) method on binary data. *Trifolium pratense* was excluded from the analysis on pollen types since only binary data was used and it was present at all sites and in all habitats.

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CHAPTER 4: HABITAT QUALITY AND RESOURCE AVAILABILITY AS PREDICTORS OF PRAIRIE BEE ABUNDANCE IN A FRAGMENTED LANDSCAPE

ABSTRACT

The spatial structure of landscape mosaics and the quality of resources within them affects how organisms utilize and disperse amongst patches of suitable habitat, yet few studies on wild bees consider the influence of habitat connectivity or differential responses to landscape composition among suites of species with different life history traits. Here, key predictors of wild bee diversity and abundance among functional groups were explored in the context of a prairie landscape with gradients of agricultural fragmentation. Bee species were categorized by sociality, nesting strategy, floral specificity, and foraging capacity and the abundances within the sites from which bees were collected were used as a proxy of forage patch utilization. Predictor variables were measures of forage patch quality and resource availability, and measures of landscape composition and connectivity taken within increasing radial distances into the landscape surrounding each study site. At the local scale, the abundance of blooming forbs and the size of a foraging patch were the best predictors of bee abundance across functional groups and were often paired with a measure of the functional connectivity of suitable habitats and the percentage of woodlands and croplands in the landscape surrounding a forage patch. The scale at which bee responses were linked to measures of connectivity and landscape composition generally corresponded to the foraging capacities of different suites of species. Additionally, the importance of woodlands or croplands was linked to differences in nesting strategy, where the former was an important predictor of wood- and cavity-nesting bees, and the latter of ground-nesters. Bee response to connectivity and

floral resources also varied among sociality and floral specificity such that the connectivity of more heterogeneous and florally rich forage patches have great importance for solitary and oligolectic bees, whereas forb abundance and connectivity were secondary for social and polylectic bees to landscape composition. The results support the idea of complementary habitat use due to patterns in nesting and floral resource availability, and that the utility of a forage patch to diverse suites of species varies with local habitat quality and landscape composition. Conservation planning for the persistence of diverse pollinator populations may therefore be greatly improved by taking a broad cross-habitat perspective that utilizes multiple metrics of habitat quality and connectivity.

INTRODUCTION

Land cover change has a primary role in biodiversity loss (Millennium Ecosystem Assessment 2005; Newbold et al. 2015) and can impair ecosystem functioning (Allan et al. 2015) through its effect on the long-term resilience of ecosystem services (Oliver et al. 2015). In grasslands, plant-pollinator interaction networks become increasingly simplified as species are lost (Brosi et al. 2007) and parallel declines in the diversities of interconnected wild bees and insect-pollinated plants have been documented (i.e. Biesmeijer et al. 2006; Anderson et al. 2011). This can result in functional depletion (Papanikolaou et al. 2017) and arises from modification of pollinator flows which affect out-crossing between plant populations in different patches (Gathmann and Tscharrntke 2002; Goverde et al. 2002).

In landscapes, the spatial arrangement and heterogeneity of natural or semi-natural habitats and various human land uses are highly influential on the survival and dispersal capacity of pollinators because these attributes dictate the distribution of resources and the permeability of the landscape (Andersson et al. 2007; Jha and Vandermeer 2010; Roulston and Goodell 2011). In other words, they determine functional connectivity. This is defined by Metzger (2001), “the capacity of a landscape or landscape units to facilitate [the] biological flows [of a given species or group].” The mosaic pattern of different patch types creates differing levels of connectivity that either enable or hinder movement through the landscape (Kreyer et al. 2004; Ekroos et al. 2008; Ricketts et al. 2008).

Because plants and pollinators are closely linked, conservation efforts of one must consider the other. Most pollinating insects are dependent on a habitat mosaic to fulfill their nesting and floral resource needs, so habitat connectivity is essential for both plants and their pollinators (Benedict and McMahon 2006). Patches of suitable habitat which serve as stepping stones, corridors, and buffers along roadsides or crop fields (i.e. habitat quality) provide opportunities for connectivity at different spatial scales (Dover and Settele 2009). Though numerous metrics of habitat connectivity have been developed, those with a graph theoretic approach based on the availability (i.e. reachability) and configuration of habitat patches are especially useful for conservation planning because they allow for the evaluation of a network of habitats to support resilient and persistent populations (Neel et al. 2014). Furthermore, variation in ecological and life-history traits among bee species results in differential perception of and interaction with available resources. Consequently, functional connectivity among fragments of suitable habitat occurs at different spatial scales for different suites of species. Sociality, nesting behavior, diet breadth and foraging capacity may all potentially influence bee responses to habitat change (Williams et al. 2010). Body size, in particular, determines the spatial scale within which species are able to operate and obtain resources from their environment (Lavorel and Garnier 2002; Larsen et al. 2005; Petchey and Gaston 2006).

This study assessed local and landscape factors which influence the abundance, species richness, and diversity of wild bees in a mosaic landscape of tallgrass prairie grasslands and agriculture. Three general questions were addressed: (i) what combination of local and landscape components best predicts bee distributions among patches of suitable habitat, (ii) does this combination differ between suites of species

according to ecological and life-history traits, and (iii) does the scale at which relevant components influence bee abundance correspond to the scale at which suites of species are expected to interact with their environment according to the estimated limits of their foraging capacities? The implications of these results are discussed in the context of conservation planning for pollination services in agriculturally intensive landscapes.

METHODS

This study explores the evidence of local and landscape factors in structuring the distribution of wild bees across the study area in order to predict reserves and deficits of pollinators and their services. Data were collected from June to August in 2012-2014.

Study area and research sites

The study location consisted of an agricultural landscape in southeastern Nebraska, with specific study sites in Johnson, Pawnee, and Richardson Counties. All sites were located within an area designated by the Nebraska Natural Legacy Project as a Biologically Unique Landscape (BUL), this one being the Southeast Prairies BUL. A total of 15 sites were selected from three of the dominant grassland types in the landscape: remnant tallgrass prairie (also referred to as haymeadow), grazed pasture, and properties enrolled in the Conservation Reserve Program (CRP). Five privately owned properties were selected for each grassland type based on management practices and landowner permission. The remnant prairies were managed for hay production, with haying occurring once per year. The grazed pastures were actively grazed by cattle

during the study, although cattle were rotated between different pastures at different times. The CRP properties were all CP25 grass/forb seed mixes at least five years into their CRP contract. These natural and semi-natural grassland patches were selected as representatives of different suitable bee habitat types within a mosaic of row crop agriculture (predominantly corn or soybeans), woodlands, and grasslands. These sites were each sampled twice in June, July, and August of 2012, and at least once in each of the same months in 2014 with the exception of two CRP sites that had been converted back to crop production after the first year of the study and were therefore not available for further sampling. The size range of these study sites was 7.6-58.4 acres.

Bee sampling and identification

Bees were sampled with blue vane traps (SpringStar® Inc., Woodinville, WA, USA) suspended from a PVC pole at the level of the vegetation. Traps were set up for 48 hours during appropriate weather conditions, with four traps assigned to each study site. The contents of each trap were transferred to Ziploc® freezer bags in the field, then placed in a freezer until specimens could be sorted and identified. Bees were identified to species when possible but some groups, such as *Lasioglossum*, were identified to morphospecies. Bees were first identified to genus using Michener et al.'s Bee Genera of North and Central America (1994) and then to species using a combination of keys on discoverlife.org, local keys to prairie bees of Missouri and a reference collection with confirmed species identifications that was created with professional assistance from Mike Arduser at the Missouri Department of Conservation, St. Louis Regional Office, St.

Charles, MO, 63304 USA. Information on bee functional traits was obtained from the same resources.

Characterization of the bee community using life history traits

Wild bee abundance, species richness, and the Shannon diversity index were calculated for each sample day. Abundance is the sum total of individuals collected with the four blue vane traps at each site and species richness is the total number of species collected from each site. Although Shannon diversity is calculated from both the number of species and their abundances, it is useful because it characterizes the evenness of the community.

Additionally, bee species were divided to categories according to certain functional traits (Table 4.1): sociality, nesting strategy, floral specificity, and foraging capacities (i.e. the distances species are able to cover to acquire sufficient forage resources). Sociality describes either *social* species or *solitary* species. Only eusocial species with a queen as the only egg-laying female and workers performing other tasks were considered *social*, but these were further categorized as *large* or *small social* species. *Solitary* species construct a nest and provision their own offspring with food. *Cleptoparasites* were considered as a separate group under nesting strategy rather than sociality. These species locate the nests of suitable hosts and lay eggs to be provisioned by the *nest-building* species. The different nesting strategies used by the nest-building bees were *cavity-nesters*, *ground-nesters*, and *wood-nesters*. *Cavity*-nesting species are hypergeic (above-ground; Oertli et al. 2005) and nest in existing natural cavities (Michener 2007). *Ground*-nesting species are endogeic (below-ground; Oertli et al.

2005) and excavate nests in the soil. *Wood*-nesting species are hypergeic and use wood or twigs to construct their nests. Wood-nesters were additionally categorized as *large* and *small* excavators. Floral specificity was defined as either *polylectic* or *oligolectic*. *Polylectic* bees are generalists and forage on numerous, unrelated forbs for pollen and *oligolectic* bees are limited to certain, typically related, pollen taxon (Michener 2007). Finally, foraging capacities were assigned to broad categories which span the range of foraging distances for solitary bees according to body size by Gathmann and Tscharrntke (2000), and for social bees as summarized by Zurbuchen et al. (2010). Foraging capacities therefore included doorstep foragers (up to 250m from nest), short- to moderate-distance foragers (250m-400m), moderate-distance foragers (400m-800m), and two long-distance foraging categories: 800m-1200m, and greater than 1200m from the nest. The short- to moderate-distance foragers were also combined into one broader group (up to 400m) because of the wide range of foraging distances documented for bees within the corresponding size ranges in previous literature (Zurbuchen et al. 2010).

Local and landscape parameters

Combinations of local and landscape parameters were used for model assessment of each response variable of the bee community (Table 4.1). Local parameters refer to habitat quality of the foraging patch from which bees were collected, presumably having traveled from nearby nesting sites in the surrounding landscape. Parameters included floral resource availability (forb abundance, density, and species richness), site area (m²), site heterogeneity (the number and density (m²) of land cover types found within a site), and the percentage of each land cover type found within each study site (grasslands,

woodlands, wetlands, and development). Floral resources were measured for each site as the number of species in bloom and the number of blooming stems within two $\frac{1}{4}$ acre plots. Forb sampling locations were randomly selected for each study site prior to each session. Density (blooming stems per m^2) was also estimated. Forb sampling occurred simultaneously with bee sampling, although an additional day was taken when needed at sites where forb density was high.

The other parameters were measured from land use and land cover (LULC) data for the area in a geographic information system (GIS) using ArcGIS[®] software and ArcMap10[™]. The LULC map was created from data with 30-meter resolution obtained from the Rainwater Basin Joint Ventures project (2012), supplemented with land cover data specifically for the Southeast Prairies BUL (Nebraska Natural Heritage Program and Northern Prairies Land Trust). The data was updated, where necessary, with ground surveys within 1200m of each study site during 2013 and 2014. Land cover types from all sources were condensed into six categories: grasslands, woodlands, wetlands, development, roads, and croplands. The percentages of grasslands, woodlands, wetlands, and development at each site were measured as local parameters. Landscape parameters included the percentage of each land cover category within 250m, 400m, 800m and 1200m of each site's perimeter. These were selected following Le Féon et al. (2013) to coincide with the approximate foraging capacities of the bee community. The number of land cover types was used as a measure of landscape composition, and landscape configuration was measured as the density of suitable nesting and forage patches within each radius.

Habitat connectivity and availability

Several measures of habitat connectivity were used as additional landscape parameters. These were calculated from the LULC map using Conefor Sensinode 2.6 software (Saura and Torné 2009). This software uses a graph-theoretical approach to quantify habitat availability and patch importance in the landscape. It also incorporates dispersal distances and behavioral responses of organisms to non-habitat components of the graph, in addition to the spatial arrangement of suitable habitats (Tischendorf and Fahrig 2000; Theobald 2006). Therefore, it can be used to measure both functional and structural connectivity. Nodes consisted of suitable nesting and forage habitats, as well as non-habitat land uses, which were assigned an area-weighted suitability score to reflect potential resource quality for wild bees. Nodes were connected through links using a probabilistic connection model and represent the potential for species to disperse between any two nodes. The threshold dispersal distances used in this study correspond to the foraging capacity intervals (250, 400, 800, and 1200 meters) used to categorize species of the bee community. For simplicity, these were used as maximum dispersal distances and hence, the direct dispersal probability value was set to 0.05 as recommended by Saura and Pascual-Hortal (2007).

The LULC map included a total of 64 cover types which were more broadly categorized both to ease the assignment of suitability scores for each node, but also to simplify the analysis to reduce computational time. All grasslands and woodlands were considered suitable habitat and the suitability score was 0.95 multiplied by patch area. The score was set high to indicate preferred habitat, but less than 100% to account for

variation between different kinds of grasslands and woodlands. Row crops, paved roads, and urban/suburban development were categorized as the most inhospitable habitat and assigned a suitability score of 0.05 multiplied by patch area. This score was set low to indicate that these are largely non-habitat compared to natural areas, and to reflect the least permeable and florally-poor conditions. Local unpaved roads and rural development were assigned an intermediate score of 0.20 multiplied by patch area to reflect marginal nesting and forage potential. The implications of this differential scoring are to reflect the gradient of resource availability for wild bees between the most and least suitable types of habitat.

Both standard inter-patch connectivity and more complex habitat availability metrics were used. Availability (i.e. reachability) indices incorporate intra-patch connectivity in addition to inter-patch connectivity of nodes. The simplest index used here was the number of links (NL), which is a binary measure of linkage between any two suitable nesting or forage patches. A pair of nodes is or is not connected for a group of bees using least-cost distance within the threshold of the relevant foraging capacity.

The integral index of connectivity (IIC) is a more complex index. It accounts for the connectivity that occurs within the node, the dispersal fluxes of individuals between nodes, and the extent to which the node serves as a stepping stone to others, thereby contributing to the connectivity of those nodes (Pascual-Hortal and Saura 2006). IIC_{Intra} and IIC_{Flux} are two independent fractions of IIC which represent the different ways in which a node might influence habitat availability. IIC_{Intra} reflects the node's available habitat area and therefore represents intra-patch connectivity, or availability (Saura and

Rubio 2010). IIC_{Flux} reflects the potential for individuals to disperse to or from other nodes, using the node of interest, in this case each study site, as either the ending point or starting point of dispersal movements (Saura and Rubio 2010). This metric, with area-weighted dispersal, describes how well the node of interest is connected in terms of flux of individuals, but not how it contributes to maintaining connectivity among other nodes in the landscape (Saura and Rubio 2010). IIC_{Intra} is actually a local parameter, as it is independent of connectivity to other habitat patches and the flow of individuals between patches. However, it's included in landscape parameters because it is a component of IIC, which accounts for movements among and links between other patches in the landscape.

Finally, generalized betweenness centrality (BC^{IIC}) integrates betweenness centrality (BC) into the integral index of connectivity. BC measures the extent to which a node serves as a central hub through which optimal paths of dispersing individuals flow, and it is measured as the sum of all shortest pathways that go through a node (Bodin and Saura 2010). BC^{IIC} expands this to account for node area and topological distance. It gives more weight to paths that are expected to carry larger flows of individuals and to those which connect larger patches, thereby giving greater ecological relevance to the BC metric (Bodin and Saura 2010). This metric could also be argued as a local parameter since it refers to a quality of the study site, like IIC_{Intra} , but its calculation involves interactions with other components of the landscape. In this study, it is used as a landscape parameter.

Statistical analysis

Multi-model inference was used to identify the most important predictors of wild bee abundance. It is a useful tool in studies with multiple potential predictors and combinations that contribute to species' abundances. An information-theoretic approach weighs the evidence supporting these models to identify those with greatest parsimony (fewest variables with maximum weight) based on information criteria. Here, I used Akaike's Information Criterion (Akaike 1973) adjusted for small sample sizes (AICc) to select top models from a candidate set that best fit the empirical data (Anderson et al. 2000; Burnham and Anderson 2002).

Selection began for each subset of wild bees by screening measures of resource availability, habitat heterogeneity, habitat connectivity, and landscape composition for collinearity and the strength of correlation to bee response variables via Pearson product moment correlations. Transformations were used where necessary to meet the assumption of normality. For terms which were measured at multiple scales (i.e. at foraging intervals between 250-1200m of each study site) and were correlated to bee response variables at multiple scales, the terms with stronger correlation coefficients which were not also significantly correlated to other terms were selected such that only a single variable was used for each type of explanatory variable for resource availability, habitat heterogeneity, and landscape composition.

The potential of these candidate variables to predict bee responses was explored in best subset regression analyses and multiple linear regression (MLR) was used to investigate how they were linked to bee response. Correlations and regressions were

performed in SigmaPlot 13 (Systat Software, San José, CA), and variables which were not necessary for predicting bee response in MLR were eliminated. The ‘dredge’ function in the MuMIn package in R ((Bartoń 2009) was applied to generate models with all possible combinations of the remaining predictors, including a null model, and rank them by Akaike’s information criterion corrected for small sample size (AICc). This was followed by ‘get.models’ with a cutoff of $\Delta AIC_c \leq 2$. With dredge, the model selection process is automated, beginning with a fitted global model. Fitting was achieved using generalized linear models (GLM) with either a Gaussian or a Poisson response distribution. Quasi-AICc (QAICc) was used with Poisson distributions where count data was overdispersed (Richards 2008). Redundant or nested models (simpler models nested within more complex versions) were removed from the candidate set to avoid low model weights and redundancy in the top model set (Grueber et al. 2011). Top model sets were averaged using the zero method (Burnham and Anderson 2002) to decrease the effect size of predictors that only appear in models with small weights. This dilutes estimates for weak predictors toward zero (Lukacs et al. 2010) and is useful when the aim of the study is to determine which factors have the strongest effect on the response variable (Nakagawa and Freckleton 2010). Model-averaged estimates were interpreted in terms of direction (positive or negative) and magnitude (effect size) in relation to one another.

RESULTS

Predictors of bee abundance, species richness, and diversity

Overall bee abundance was best predicted by a combination of blooming forb abundance, the size of a study site, and the percentage of woodlands and croplands in the

surrounding landscape. These comprise the top two models for bee abundance, with a combined model weight of 79% (Table 4.3). The dispersal potential to or from a study site was less influential, with an importance value of 0.21 (Table 4.4). Woodlands held greater importance than croplands (Table 4.4; 0.56 vs. 0.44), but forb abundance is the primary predictor of bee abundance in this study and is a component of each of the three models in the top model set (Table 4.4; estimate = 0.404 ± 0.063). The combined model weights of 100% (Table 4.3), suggest that this combination of predictors is well supported by the data.

In contrast, a single predictor variable, the percentage of croplands within 400 meters of a study site (Crops.400m) was the only to hold any importance for bee species richness (Tables 4.3 and 4.4). Since this was followed closely by the null model, with 51% and 49%, respectively, predictors were only weakly supported by the data for this response. Similar to predictors of bee abundance, the species richness of blooming forbs (Frb.Rich) is strongly supported as a predictor of wild bee diversity, especially when accompanied by generalized betweenness centrality (BCIIC; the extent to which a site acts as a stepping stone to other suitable habitat patches) within 800 meters of the study site (Table 4.3, combined model weight of 100%), although connectivity's importance, at 0.58, was secondary to forb richness (Table 4.4).

Predictors of social and solitary bee abundances

Social and solitary bee abundances were both influenced by a combination of floral resource quality, habitat composition, and connectivity. The percentage of wetlands and woodlands within 800 meters of a study site were the strongest predictors

and 68% of model weight. This was followed by forb abundance and the dispersal potential to or from other suitable habitat patches which account for the remaining 32% (Table 4.5). Local habitat quality, measured as blooming forb abundance and the size of a study site were the best predictors of large social bee abundance, comprising 79% of top model weights, whereas small social bee abundance was best predicted by landscape composition (Table 4.5). The latter was measured as the percentage of woodlands and wetlands in the landscape surrounding a study site and each predictor was of equal importance at 0.92 (Table 4.6). For solitary species, habitat connectivity (BCIIC), the species richness of blooming forbs, and the amount of woodland cover within a study site comprised the top model, with 74% of model weight (Table 4.5). The reachability of a forage patch and diversity of floral resources are important predictors of this functional group, whereas connectivity appears to be secondary for social species and the quantity of floral resources is a better predictor.

Predictors of nest-building and cleptoparasitic bee abundances

Woodlands and connectivity were also important predictors of bee abundance when categorized by nesting strategy, but in this case the relevant measure of connectivity was Flux, the dispersal potential to or from a study site within 800 and 400 meters for cleptoparasites and nest-builders, respectively (Table 4.7). Forb abundance was an additional predictor of nest-building bee abundance, and held equal importance to connectivity (Table 4.8, 1.00), and the top two models, with either woodlands or croplands in the landscape surrounding a study site, held 74% of the weight in the top model set (Table 4.7).

Among the nest-builders, forb abundance, a measure of habitat connectivity, and the percentage of woodland cover in the surrounding landscape were the most frequently encountered predictors of wild bee abundance (Table 4.9). Two models comprised the top model set for predicting ground-nesting bee abundance, with little difference in weights for forb abundance and the size of a study site (52%) or the percentage of croplands within 250 meters of the site and forb abundance (48%; Table 4.9). Forb abundance held the greatest importance, followed by connectivity and crop cover (1.00, 0.52, and 0.48, respectively; Table 4.10). Wood-nesting bees (large and small species combined) were primarily influenced by forb abundance, which alone comprised the top model with 73% of model weight, followed by woodland cover within 1200 meters of the site with the remaining 27% of model weight (Table 4.9). Within the wood-nesters, the top model for predicting large species abundances was comprised of the dispersal potential to or from the site (Flux.250m) and the percentage of woodlands within 1200 meters of the site, which held 78% of model weight (Table 4.9). Small species abundances were best predicted by the generalized betweenness centrality of a study site (BCIIC.250m) and forb abundance (73%; Table 4.9). The scale at which woodlands were relevant to wood-nesting bee abundance corresponded to bee size, with the smaller species being influenced by the percentage of woodlands within 400 meters, and 1200 meters for large. However, the woodland variable held less importance for small wood-nesters than large (0.27 and 0.78, respectively; Table 4.10). For cavity-nesters, landscape composition, particularly the percent of the landscape with woodland cover within an 800-meter radius, was the best predictor of bee abundance, and held 59% of model weight when accompanied by the percentage of wetlands the roads (Table 4.9).

Predictors of polylectic and oligolectic bee abundances

Connectivity within 800 meters of the site was important for both polylectic and oligolectic bees, but this was dispersal potential combined with forb abundance for the former, which held 90% of the model weight, and number of links to other suitable patches for the latter, which held only 32% of model weight (Table 4.11). It was also secondary, for oligolectic bees to the percentage of development within 400 meters surrounding the study site, and heterogeneity of the site, which comprised the top model with 39% of the weight, compared to 32% for connectivity alone (Table 4.11). The inclusion of the null model in the confidence set suggests a poorer fit of the data, so bees with greater floral specificity may be better predicted by other factors not considered in this study. Still, the three predictors collectively hold 71% of the weight, and held similar importance for oligolectic abundance (Table 4.12; 0.39 for site heterogeneity and the percentage of developed land cover, and 0.32 for connectivity).

Predictors of abundance of bees with different foraging capacities

Woodlands were a relevant predictor of bee abundance within all foraging ranges of up to 800 meters (Table 4.14). For those that are able to forage at distances of 1200 meters or greater, habitat connectivity, measured as dispersal potential, held the majority of top model weights at 69% and 49% for these two groups, respectively (Table 4.13). Habitat connectivity was also an important predictor of bee abundance for groups with 400- and 800-meter foraging capacities, only measured in these models as generalized betweenness centrality (Table 4.13) and was the strongest predictor for both groups (Table 4.14; estimates of BCIIC for 400- and 800m foraging capacities = 0.703 ± 0.342

and 0.661 ± 0.059 , respectively). The scale at which landscape composition and habitat connectivity measures were linked to bee responses generally corresponded with the foraging capacities by which bees were categorized; smaller bees with shorter expected foraging ranges were best predicted by measures taken within the smallest radial distances, and larger bees with greater foraging ranges were better predicted by these measures taken at longer distances. The exception was the 800-1200 meter range, for which dispersal potential within 400 meters was the best predictor (Table 4.13).

Connectivity measures held the greatest importance for all of the models in which they were included, although the composition of woodlands and croplands in the surrounding landscape were either of equal importance to connectivity for predicting bee abundances, or close to it for all groups except for the greatest foraging distance, in which land composition importance was only 0.18, compared to 0.49 for connectivity (Table 4.14).

DISCUSSION

In landscapes dominated by intensive agricultural practices, negative impacts on pollinators have been well documented (Kearns et al. 1998; Steffan-Dewenter et al. 2005). However, considering the wild bee community of the Southeast Prairies as a whole, encompassing all functional groups, the percentage of croplands was often a positive predictor of bee abundance, albeit of less importance than the percentage of woodlands, especially when combined with measures of habitat connectivity and floral resource availability. Here, study sites were presumed to be used for foraging and bee abundances, species richness, and Shannon diversity estimates were used as a proxy of

the extent to which a site is utilized by the wild bee community. Differences in responses between functional groups arise from the traits specific to each group and can be examined as a reflection of how gradients in habitat suitability and availability influence the distribution of species. The results suggest that the structure of this agricultural mosaic is able to support a diverse bee community so long as patches of forage habitat are of high quality and are well connected at multiple functional scales.

Predictors of wild bee abundance, species richness, and diversity

Although models predicting wild bee species richness were only weakly supported by the data in this study, floral resource availability was an important predictor for both overall bee abundance and Shannon diversity. Bee abundance was greater where blooming forb abundance was higher, and this fits with previous work in which floral resource availability is considered a driver of wild bee abundance and diversity (Potts et al. 2003; Roulston and Goodell 2011). Here, bee diversity estimates were greater when more species were in bloom and when patches within a distance of 800 meters were well connected. Previous studies have demonstrated the link between persistent diverse plant communities and pollinator diversity, even when some forbs might only be visited in low frequencies (Tuell et al. 2008). Numerous others are highly attractive and are visited in great numbers (Corbet et al. 1994; Frankie et al. 2005; Carvel et al. 2006).

The percentage of woodlands in the surrounding landscape was also an important predictor of wild bee abundance in the Southeast Prairies. Woodlands are considered an important forage source during the spring in temperate regions (Tuell et al. 2008; Westwood 2006), especially for species within *Andrena*, *Colletes*, and *Osmia* (Stubbs et

al. 1992), since many tree species flower in the spring, but may be of limited utility as forage for the remainder of the season (Mandelik et al. 2012). However, the importance of woodlands in this landscape may lie in the provisioning of nesting substrates for a variety of bees, as well as in the edge effects that woodland structure creates, which can greatly influence the survival and fitness of some species (Vallet et al. 2010; Wright et al. 2010).

Predictors of social and solitary bee abundances

Woodlands were an important component of landscape composition for both social and solitary bees. On-site woodlands were important to solitary bee abundance whereas greater social bee abundances occurred at sites with more woodlands within 800 meters in the surrounding landscape. Lentini et al. (2012) found a positive correlation of both bee species richness and abundances to the number of trees within a patch, similar to the greater solitary bee abundances found at sites with a greater percentage of woodland cover in this study. The importance of on-site woodlands may be due to the dual environments that site heterogeneity offers. The trees and other woody plants provide alternative structure for nesting while the open grassland component provides floral resources for forage (Vallet et al. 2010; Wright et al. 2010). Similarly, wetlands offer rich floral resources and Bergh (2011) demonstrated a positive correlation between floral resource availability and bee abundance within wetlands. Wetlands have been demonstrated to be valuable to bumble bees, in particular because of the presence of willow in early spring, which provide newly emerged queens with the pollen resources required to establish successful nests at a critical stage in the bumble life cycle (Sepp et

al. 2004). Other research found faunal differences in the bee community between wet and dry grasslands, but the difference was linked to feeding specialization rather than nesting preferences (Moroń et al. 2008).

In this study, the differences in the types of predictors for social versus solitary bees' abundances may reflect differences in the tendency to forage based on quantity or quality. Social species' abundance was greater in larger sites and those with higher forb abundance. In contrast, solitary species were better predicted by forb richness, possibly due to a preference for variety in floral resources over the quantity of floral resources, especially since the reachability of a forage patch was also important to this functional group but was of secondary importance to social species. These groups employ very different foraging strategies as central place foragers, with social species able to orchestrate effort to both meet the varying demands of a colony and adjust for variation in resource availability over the flowering season. Solitary species, on the other hand, must be able to adapt their strategy amidst these fluctuations in resource availability as a solo endeavor. Without conspecifics to share the burden of locating and gathering resources to bring back to the nest to support reproduction, solitary species may seek variety, and therefore different quality, over quantity to maximize the potential gain of their foraging efforts. Although little is currently known about the nutritional requirements of non-*Apis* and non-*Bombus* species (Vaudo et al. 2015), most bees are solitary and exhibit some degree of floral specificity (oligolecty) (Roulston and Cane 2008). Considering the range of differences in life history traits, brood production, and social structure it is likely that different species have varying quantitative and qualitative

nutritional requirements to successfully reproduce and persist in an ecosystem (Vaudo et al. 2015).

Regardless of potential differences in resource selectivity between social and solitary species, positive species-area relationships are commonplace in ecology (MacArthur and Wilson 1967; Lomolino 2000). Larger patches tend support greater numbers and more diverse assemblages of species than small patches (Tschardt and Brandle 2004). Both species richness and the number of interactions in pollination webs increase not only with proximity to neighboring suitable habitat, but also with habitat area (Sabatino et al. 2010).

Predictors of nest-building and cleptoparasitic bee abundances

Woodlands and connectivity were the strongest predictors of both cleptoparasitic bees and nest-building bees, but forb abundance was more important to nest-builders than parasites. This makes sense considering the lifestyle of cleptoparasites. These bees do not build their own nests or provide pollen to their young. Rather, they exploit the efforts of nest-building species that behave as central-place foragers (Michener 2007). Therefore, the extent of nesting resources for host species may be more important than forage to this guild since they do not exert effort locating and gathering resources for rearing brood. However, cleptoparasitic species, as well as solitary species, are more sensitive to the loss of natural habitat than social species (Jauker et al. 2013), and they are useful as an indicator species. Their presence is evidence that the host species of the bee community exist in sufficient numbers to be able to support not only their own offspring, but those of the parasites, at a level that both are able to persist.

Among nest-building bees, in addition to forb abundance and habitat connectivity, the best predictors of abundance corresponded to land cover types likely to satisfy nesting resource requirements. The percentage of croplands surrounding forage sites was important for ground-nesting bees, and the percentage of woodland cover was important for both wood- and twig-nesting groups and cavity-nesters.

Row crops (corn and soybeans) and roadways were expected to negatively influence wild bees. These types of cultivation do not provide forage for wild bees, and worse, pesticides used on corn, especially systemic neonicotinoids, have been shown to reduce foraging success and to cause mortality in honey bees (Henry et al. 2012). Cropland may be important to ground-nesting species specifically because they offer ample nesting substrate with open ground. Mining bees in Europe are known to nest on field paths, especially those with sparse vegetation and exposed soil (Westrich 1996), and many species have been observed to nest alongside crop fields (Matthewson 1968). Kim et al. (2006) found that although most species are negatively affected by agricultural intensification, it is to varying degrees. Ground-nesting bees will nest in sunflower but the abundance of nesting bees was higher where there were greater amounts of nearby natural habitat (Kim et al. 2006). Other studies have shown that agriculture is not uniformly negative for wild bee diversity (Kremen et al. 2002; Tscharntke et al. 2005; Greenleaf and Kremen 2006). Recently, Forrest et al. (2015) found greater species richness of ground-nesting bees in organic cultivation than in natural habitat, suggesting that some bees are limited by nest site availability (Steffan-Dewenter and Schiele 2008) and that the lack of suitable nest sites on farms for species of other nesting strategies filters such bees from cultivated habitats (Williams et al. 2010; Hoiss et al. 2012).

Similarly, Le Féon et al. (2010) found that wild bees respond positively to agriculture in the context of flowering crops, but negatively to livestock agriculture where permanent grasslands are modified to provide forage to support animal husbandry.

The importance of woodlands to wood-nesting groups and cavity-nesters is also not surprising. In a grassland restoration study, it was thought that low abundances of cavity-nesting bee species was due to the study sites having very little woody habitat, since it offers pre-existing cavities for nesting (Richards et al. 2011). There are also strong associations between bumble bee abundance and woodlands, particularly the extent of forest edge along the ecotone between cropland and forest (Sepp et al. 2004) and the structure of this zone may be useful to bees in a number of ways. Bumble bees, for example, may use treelines as landmarks along which to orient themselves since they tend to use such linear structures when foraging in agricultural landscapes (Cranmer 2004). Queen bumble bees also search along woodland edges for nesting sites (Svensson et al. 2000), and seem to prefer the edge since higher bumble nest densities are found along this ecotone than inner woodlands (Osborne et al. 2008).

Roads were also an important predictor of cavity-nesting bee abundance, and were the only negatively linked predictor across the bee community in this study. Similar to the consequences of intensely managed agricultural landscapes, management of roadside vegetation may be especially harmful (Johst et al. 2006), particularly excessive mowing, which has been implicated in bumble bee decline (Rasmont et al. 2006). Roads may cause some level of mortality from vehicles (Munguira and Thomas 1992), contributing to fragmentation (Trombulak and Frissell 2000), by forming barriers to inter-

patch movement (Valtonen and Saarinen 2005), and through the prevalence of invasive species (Hopwood 2008). Some pollinators are known to avoid crossing roads (Powell et al. 2007), and so the presence of these features may restrict dispersal movement among suitable habitat patches. However, roadsides may also be developed as important marginal habitat that serve to reconnect fragmented landscapes when managed appropriately.

Predictors of polylectic and oligolectic bee abundance

Habitat connectivity was an important predictor of both polylectic and oligolectic bee abundances in the Southeast Prairies, but while floral resource availability was more strongly linked to generalists, the percentage of development in the landscape surrounding a study site was more important for species with greater floral specificity. Oligolectes in other studies have been associated with wetlands, rather than dry grassland habitats, presumably due to the unique floral composition of wet meadows, (Moroń et al. 2008), but in other work in agricultural areas, small, linear remnants of vegetation and the proximity of conservation land contribute unique, and specialized species to regional bee diversity (Letini et al. 2012). Sydenham et al. (2014) used total plant cover as a measure of site suitability, which was associated with a higher proportion of pollen specialists when dominated by Ericaceae species.

Development in this study included both rural and urban or suburban development types and was included as another dimension of anthropogenic land uses that contribute to habitat loss and fragmentation. One of the primary differences in habitat change due to agriculture versus urbanization is that the latter results in greater

habitat diversity on a finer scale even though it is an ultimately more heavily modified environment (Gill et al. 2007). Previous work found greater bee species richness and abundance within rural development types than suburban, but that these decreased with greater area of “built” landscape (Bates et al. 2011). Mowed lawns may actually be quite suitable for ground-nesting bees, but mowing removes floral and structural diversity in vegetation (Morris 2000), and results in residential areas having much less forage and nesting habitat. Gardens, however, have potential to provide both nesting and forage resources in suburban landscapes (Fetridge et al. 2008). Development, especially rural development, contributes to variety in land cover types and other studies have shown that landscape heterogeneity is positively associated with bee species richness (Andersson et al. 2013). Furthermore, rural development is likely to offer specialty crops, particularly squashes, from residential gardens for oligolectic species, such as *Xenoglossa* species and *Peponapis pruinosa*, which specialize on these plants. The abundance of these bees in pumpkin, regardless of neighboring natural areas, can be high enough within the field to fulfill all pollination requirements of the crop (Julier and Roulston 2009).

Predictors of abundance of bees with different foraging capacities

Although it's recognized that community composition is influenced by variation in habitat quality from the local patch scale to the landscape scale depending on species' size and dispersal capacities (Haskell et al. 2002; Thomas 2000), most invertebrates are expected to be more influenced by patch characteristics than landscape characteristics (Mazerolle and Villard 1999). Here, however, the scale at which relevant predictors were important to bee abundance broadly corresponds to foraging capacities in that the scales

at which landscape components were measured generally increased with the capacity of bees to travel farther distances while foraging. Previous work has demonstrated that foraging effort of insect pollinators is concentrated within patches of high floral density (Westphal et al. 2003; Hegland and Totland 2005; Hegland and Boeke 2006) and Tuell et al. (2008) describe how wild bees in particular, search for patches with greater floral abundance, which maximizes the benefit of foraging effort over the costs. Larger social bees, such as bumble bees have larger resource needs that must be obtained within their foraging range than small social species with shorter foraging capacities (Greenleaf et al. 2007). The latter are comprised of social Halictidae and are expected to respond to more local conditions (Hopfenmüller et al. 2014) while the former are better able to respond to forage availability at the landscape scale (Westphal et al. 2003; Lepais et al. 2010). All groups exhibit some variation in foraging capacity, however, and despite proportional abundance to patch size patterns in other studies, bumble bees have also been known to respond more to patch quality and landscape context than to habitat size (Heard et al. 2007).

Previous research has shown that pollinator abundance in agricultural landscapes is affected by the amount of natural and semi-natural habitat surrounding a patch (Tscharntke et al. 2005), and that both the species richness and the number of interactions in pollination webs increase with proximity to other suitable habitats (Sabatino et al. 2010). Therefore, this heterogeneity in the landscape is important for preserving biodiversity in agricultural landscapes (Tscharntke et al. 2005), especially for the conservation of wild bees (Kremen et al. 2007), and many species seem to persist well in less intensively managed agricultural landscapes (Mayfield and Daily 2005; Tscharntke

et al. 2005). This persistence may result, in part, from complementary habitat use over time that corresponds to spatiotemporal patterns in floral resource availability (Mandelik et al. 2012). Diverse suites of species are only able to exploit resources among complimentary habitats if these patches are well enough connected that a wide range of foraging capacities is able to operate across the landscape. Here, the scale at which habitat connectivity best predicted bee abundances for those groups in which it was a relevant predictor was reflective of the typical ranges in which different suites of wild bees are able to forage.

The use of multiple connectivity measures in this study was worthwhile since the spatial structure of mosaic landscapes affects population dynamics and species interactions by influencing how species can move among suitable habitat patches (i.e. connectivity; Meriam 1984). Positive relationships between habitat connectivity and pollinators have been shown for butterflies (Brückmann et al. 2010) but connectivity studies on wild bees are currently few and have not shown an appreciable influence on species richness (Menses Calvillo et al. 2010; Öckinger et al. 2012; Steffan-Dewenter 2003) until recently (i.e. Hopfenmüller et al. 2014). The latter showed a negative association of habitat connectivity with total wild bee abundance, nest-building bee abundance, habitat generalists, and both large and small social species (Hopfenmüller et al. 2014). In contrast, relevant measures of habitat connectivity used in this study were generally strong predictors of bee abundances across many functional groups and the relationships were always positive.

Conclusion

The inclusion of multiple connectivity metrics in this analysis, and graph-theoretic metrics in particular, may have allowed for better identification of the network components that are important to different suites of species based on landscape composition, habitat quality, and the resource requirements of species.

Resource availability affects wild bees at both the local and landscape scales and the combination of factors that best predicts bee abundance differs among suites of species according to natural history and behavioral traits. However, the overall results of this study cross all functional groups, abundance was to support and maintain pollination services from a diverse community of wild bees, conservation efforts should focus on large, high quality forage sites that serve as stepping stones to other suitable habitats, especially woodlands within moderate- to long-distance foraging ranges.

The abundance of blooming forbs is a particularly important component of habitat quality for bees and preserving high quality forage habitat should be a conservation priority. Connectivity between resource-rich heterogeneous habitats is important for keeping disjointed patches accessible to multiple suites of species so that necessary resources can be obtained. Croplands, particularly field margins, may be less inhospitable than previously thought, at least in this context, where natural habitats are less fragmented than in the landscape outside the borders of the Southeast Prairies BUL. However, because the amount of neighboring cropland also had negative influence on certain guilds it should not be considered to have negligible impact on the wild bee community, especially since many facets of agriculture, such as tillage and chemical use,

were not specifically examined in this study. Woodlands, however, particularly forest edge, should be considered an important element in conservation plans to maintain or enhance nesting resources for wild bees. Future work may further our understanding of resource quality by assessing not only how the extent of these land cover types influences species richness, diversity, and abundance of wild bees, but also whether variation within these categories influences bees according to species' requirements. Such information may be useful for constructing context-specific management plans in tallgrass prairie landscapes and making better informed decisions on land use in conservation planning.

Table 4.1. Variables of habitat quality and landscape composition used in multi-model inference to predict bee abundance and diversity in the Southeast Prairies Biologically Unique Landscape. Descriptions of bee response variables and the parameters used to identify important predictors of abundance and diversity across a tallgrass prairie landscape are listed.

Variable type	Measurement/Parameter	Description of parameters
Bee community measures	Abundance	Total of individuals collected from each site
	Species richness	Number of species collected at each site
	Shannon entropy	Index used to estimate diversity at each site
Functional composition of bee community	Sociality	All eusocial bees (large and small species)
		Solitary bees
	Nesting strategy	Cleptoparasitic bees
		Nest-building bees
		Ground-, wood-, and cavity-nesting bees
		Large and small wood-nesting bees
	Floral specificity	Polylectic and oligolectic bees
	Foraging capacity	≤ 250m, 250-400m, 400-800m, 800-1200m, and > 1200m
Local parameters (site descriptors)	Forb abundance	Number of blooming stems measured at each site
	Forb density	Number of blooming stems per m ²
	Forb richness	Number of forb species in bloom
	Site area	Area of each site (m ²)
	S.LCTs (site heterogeneity)	Number of land cover types within a site
	S.Het.A (site heterogeneity)	Density of land cover types (per acre) within a site
Landscape parameters (measured within 250, 400, 800, and 1200m of sites)	Grasslands	% of grasslands, includes pasture, CRP, prairie
	Woodlands	% of any woodlands within each range of a site
	Wetlands	% of wetlands, includes ponds, rivers, marsh, etc.
	Development	% of rural development (homesteads, barns, etc.)
	Roads	% of roadways (dirt, gravel, and paved roads)
	Croplands	% row crops (includes corn, soybean, wheat, etc.)
	Land cover types	Total number of land cover types
	Configuration	Density of suitable nesting and forage patches
Habitat connectivity (measured within 250, 400, 800, and 1200m of sites)	NL (number of links)	Links from study sites to any suitable habitat patch
	IIC (integral index of connectivity)	Integral index of connectivity
	Intra and Flux	Two independent fractions of IIC
	BCIIC (generalized betweenness centrality)	Integrates betweenness centrality into the integral index of connectivity

Table 4.2. Results of model selection for bee abundance, species richness and Shannon diversity estimates. Listed are models within two AIC units of the top model, which include local and landscape factors that influence bee response.

Model	K^a	(Q)AICc ^b	$\Delta(Q)AICc^c$	wi^d
Abundance (QAICc)				
Crops.400m + Frb.Ab + S.Area	4	58.54	0.00	0.44
Frb.Ab + S.Area + Wood.800m	4	59.03	0.49	0.35
Flux.800m + Frb.Ab + Wood.800m	4	59.99	1.45	0.21
Species richness (AICc)				
Crops.400m	2	91.44	0.00	0.51
<i>Null</i> (intercept only)	1	91.52	0.08	0.49
Shannon diversity (AICc)				
BCIIC.800m + Frb.Rich	3	18.15	0.00	0.58
Frb.Rich	2	17.49	0.66	0.42

Notes: ^{a-d} K —The number of model parameters; AICc = Akaike's Information Criterion adjusted for small sample size or QAICc = quasi-AICc for overdispersed models; $\Delta(Q)AICc$ = relative (Q)AICc; wi = Akaike weight; Codes are given for predictors and include the abundance (Frb.Ab) and species richness (Frb.Rich) of blooming forbs at each study site, site area (S.Area), habitat connectivity (dispersal potential (Flux) and generalized betweenness centrality (BCIIC) within 800m of the sites), and the percentage of croplands (Crops) and woodlands (Wood) within 400 and 800 meters of the study sites.

Table 4.3. Model-averaged coefficients and parameter importance for predictors of bee abundance, species richness, and Shannon diversity estimates. Parameter importance and the number of models in which each parameter appeared are listed.

Coefficients (model-averaged)			95% Confidence Interval		Parameter Importance	
Parameter	Estimate	S.E.	lower	upper	Importance	N Models
Bee abundance						
Frb.Ab	0.404	0.063	0.281	0.527	1.00	3
S.Area	0.248	0.132	0.249	0.381	0.79	2
Wood.800m	0.124	0.112	0.165	0.278	0.56	2
Crops.400m	0.211	0.106	0.159	0.263	0.44	1
Flux.800m	0.065	0.023	0.258	0.347	0.21	1
Species richness						
Crops.400m	0.072	0.046	-0.041	0.325	0.51	1
Shannon diversity						
BCIIC.800m	0.063	0.059	0.007	0.225	0.58	1
Frb.Rich	0.012	0.006	-0.280	0.038	1.00	2

Notes: Adjusted S.E. are listed for each estimate. Parameter importance is calculated from the number of models and the weight of the models of the candidate set in which the parameter appears. Codes are given for predictors and include the abundance (Frb.Ab) and species richness (Frb.Rich) of blooming forbs at each study site, site area (S.Area), habitat connectivity (dispersal potential (Flux) and generalized betweenness centrality (BCIIC) within 800m of the sites), and the percentage of croplands (Crops) and woodlands (Wood) within 400 and 800 meters of the study sites.

Table 4.4. Results of model selection for social and solitary bee abundance. The candidate set consists of all models within two AIC units of the top model for predicting all social species, large and small social species, and solitary species abundances. Factors with negative effects are shown in italics.

Model	K ^a	(Q)AICc ^b	$\Delta(Q)AICc^c$	wi ^d
All eusocial bees (QAICc)				
Wood.800m + Wet.800m	3	47.21	0.00	0.68
Frb.Ab + Flux.400m	3	48.76	1.55	0.32
Large social bees (AICc)				
Frb.Ab + S.Area	3	26.12	0.00	0.44
S.Area	2	26.58	0.47	0.35
Flux.1200m	2	27.67	1.56	0.20
Small social bees (AICc)				
Wet.400m + Wood.800m	3	113.02	0.00	0.92
Solitary bees (QAICc)				
BCIIC.250m + Frb.Rich + S.Wood	4	33.34	0.00	0.74
BCIIC.250m + Frb.Rich	3	35.48	2.14	0.26

Notes: ^{a-d} K—The number of model parameters; AICc = Akaike's Information Criterion adjusted for small sample size or QAICc = quasi-AICc for overdispersed models; $\Delta(Q)AICc$ = relative (Q)AICc; wi = Akaike weight; Negative effects are shown with italics. Codes are given for predictors and include habitat connectivity (the dispersal potential to or from a study site (Flux) and generalized betweenness centrality (BCIIC)); landscape composition (percentage of woodlands (Wood) and wetlands (Wet) in the landscape surrounding a study site); the abundance (Frb.Ab) and species richness (Frb.Rich) of blooming forbs at each study site; the size of a study site (S.Area); and the percentage of a study site with woodland cover (S.Wood). The distances given (250m, 400m, and 800m) refer to the scale at which measures of connectivity and landscape composition were relevant to bee responses.

Table 4.5. Model-averaged coefficients and importance of predictors of social and solitary bee abundance. Estimates \pm standard error, confidence intervals, predictor importance and the number of models in which each variable appears are listed. Negative effects are shown in italics.

Coefficients (model-averaged)			95% Confidence Interval		Parameter Importance	
Variable	Estimate	S.E.	lower	upper	Importance	N Models
All eusocial bees						
Wood.800m	0.346	0.238	0.409	0.601	0.68	1
Wet.800m	0.324	0.223	0.385	0.561	0.68	1
Flux.400m	0.136	0.046	0.343	0.522	0.32	1
Frb.Ab	0.123	0.052	0.288	0.494	0.32	1
Large social bees						
Frb.Ab	0.205	0.257	-0.043	0.966	0.44	1
S.Area	0.482	0.342	0.079	1.132	0.80	2
Flux.1200m	0.112	0.257	-0.028	1.121	0.20	1
Small social bees						
Wet.400m	0.395	0.106	0.199	0.596	0.99	1
Wood.400m	0.482	0.122	0.257	0.712	0.99	1
Solitary bees						
BCIIC.250m	0.529	0.058	0.415	0.643	1.00	2
Frb.Rich	0.454	0.039	0.378	0.530	1.00	2
S.Wood	0.281	0.167	0.314	0.442	0.74	1

Notes: Adjusted S.E. are listed for each estimate. Negative parameters with are shown in italics. Parameter importance is calculated from the number of models and the weight of the models of the candidate set in which the parameter appears. Codes are given for predictors and include habitat connectivity (the dispersal potential to or from a study site (Flux) and generalized betweenness centrality (BCIIC)); landscape composition (percentage of woodlands (Wood), wetlands (Wet), and croplands (Crops) surrounding a study site); the abundance (Frb.Ab) and species richness (Frb.Rich) of forbs at each study site; the site size (S.Area); and the percentage of a site with woodland cover (S.Wood). The distances given (250m, 400m, and 800m) refer to the scale at which measures of connectivity and landscape composition were relevant to bee responses.

Table 4.6. Results of model selection for cleptoparasitic and nest-building bees. The candidate set consists of all models within two AIC units of the top model for predicting cleptoparasitic and nest-building species abundances.

Model	K ^a	(Q)AICc ^b	$\Delta(Q)AICc^c$	wt ^d
Cleptoparasitic (cuckoo) bees (QAICc)				
Flux.800m + Wood.400m	3	29.08	0.00	0.73
Flux.800m	2	31.03	1.95	0.27
Nest-building bees (QAICc)				
Flux.400m + Frb.Ab + Wood.800m	4	58.04	0.00	0.38
Crops.400m + Flux.400m + Frb.Ab	4	58.13	0.09	0.36
Flux.400m + Frb.Ab	3	58.78	0.74	0.26

Notes: ^{a-d} K—The number of model parameters; AICc = Akaike's Information Criterion adjusted for small sample size or QAICc = quasi-AICc for overdispersed models; $\Delta(Q)AICc$ = relative (Q)AICc; wt = Akaike weight; Codes are given for predictors and include the abundance of blooming forbs (Frb.Ab); the dispersal potential to or from a study site within 400 and 800 meters (Flux); and the percentage of cultivation (Crops) and woodlands (Wood) within 400 and 800 meters of the study site.

Table 4.7. Model-averaged coefficients and importance for predictors of bee abundance for cleptoparasites and nest-building species. Estimates \pm standard error, confidence intervals, predictor importance and the number of models in which each relevant variable appears are listed.

Coefficients (model-averaged)			95% Confidence Interval		Parameter Importance	
Variable	Estimate	S.E.	lower	upper	Importance	N Models
Cleptoparasitic (cuckoo) bees						
Flux.800m	1.084	0.297	0.503	1.666	1.00	2
Wood.400m	0.440	0.363	0.049	1.163	0.72	1
Nest-building bees						
Flux.400m	0.311	0.044	0.349	0.486	1.00	3
Frb.Ab	0.387	0.054	0.424	0.541	1.00	3
Wood.800m	0.076	0.099	0.315	0.437	0.38	1
Crops.400m	0.069	0.094	0.239	0.346	0.36	1

Notes: Adjusted S.E. are listed for each estimate. Parameters with a negative influence are shown in italics. Parameter importance is calculated from the number of models and the weight of the models of the candidate set in which the parameter appears. Codes are given for predictors and include the abundance of blooming forbs (Frb.Ab); the dispersal potential to or from a study site within 400 and 800 meters (Flux); and the percentage of cultivation (Crops) and woodlands (Wood) within 400 and 800 meters of the study site.

Table 4.8. Results of model selection for nest-building bees. The candidate set consists of all models within two AIC units of the top model for predicting ground-, wood-, and cavity-nesting bee abundances. Factors with negative effects are shown with italics.

Model	K^a	(Q)AICc ^b	$\Delta(Q)AICc^c$	wi^d
Ground-nesting bees (QAICc)				
Frb.Ab + S.Area	3	29.87	0.00	0.52
Crops.250m + Frb.Ab	3	30.04	0.17	0.48
Wood-nesting bees (QAICc)				
Frb.Ab	2	28.91	0.00	0.73
Wood.1200m	2	30.92	2.02	0.27
Large wood-nesting bees (AICc)				
Flux.250m + Wood.1200m	3	26.77	0.00	0.78
S.Area + Wood.1200m	3	29.31	2.54	0.22
Small wood-nesting bees (QAICc)				
BCIIC.250m + Frb.Ab	3	15.99	0.00	0.73
Frb.Ab + Wet.800m + Wood.400m	4	17.99	1.99	0.27
Cavity-nesting bees (AICc)				
Wood.800m + Wet.1200m + <i>Rds.400m</i>	4	23.06	0.00	0.59
Wood.800m + <i>Rds.400m</i>	3	23.81	0.75	0.41

Notes: ^{a-d} K—The number of model parameters; AICc = Akaike's Information Criterion adjusted for small sample size or QAICc = quasi-AICc for overdispersed models; $\Delta(Q)AICc$ = relative (Q)AICc; wi = Akaike weight; Codes are given for forb abundance (Frb.Ab), site area (S.Area), habitat connectivity (dispersal potential (Flux.250m) and generalized betweenness centrality (BCIIC.250m)), the configuration of suitable habitats (Config.250m); and the percentage of cropland (Crops.250m), roads (*Rds.400m*), wetlands (Wet.800m) and woodlands (Wood.400m, Wood.800m, and Wood.1200m) in the surrounding landscape.

Table 4.9. Model-averaged coefficients and importance of predictors of nest-building bee abundances. Estimates \pm standard error, confidence intervals, predictor importance and the number of models in which each variable appears are listed for ground-, wood-, and cavity-nesting species. Factors with negative effects are shown in italics.

Coefficients (model-averaged)			95% Confidence Interval		Parameter Importance	
Variable	Estimate	S.E.	lower	upper	Importance	N Models
Ground-nesting bees (QAICc)						
Frb.Ab	0.441	0.054	0.335	0.548	1.00	2
S.Area	0.176	0.170	0.282	0.395	0.52	1
Crops.250m	0.158	0.166	0.274	0.386	0.48	1
Wood-nesting bees (QAICc)						
Frb.Ab	0.450	0.284	0.427	0.801	0.73	1
Wood.1200m	0.126	0.214	0.298	0.647	0.27	1
Large wood-nesting bees (AICc)						
Wood.1200m	0.629	0.420	0.242	1.371	1.00	2
Flux.250m	0.728	0.294	0.151	1.304	0.78	1
S.Area	0.155	0.327	0.094	1.319	0.22	1
Small wood-nesting bees (AICc)						
BCIIC.250m	0.343	0.264	0.098	0.842	0.73	1
Frb.Ab	0.629	0.235	0.168	1.091	1.00	2
Wet.800m	0.129	0.233	0.108	0.847	0.27	1
Wood.400m	0.116	0.213	0.035	0.828	0.27	1
Cavity-nesting bees (AICc)						
Wood.800m	0.545	0.229	0.096	0.993	1.00	2
<i>Rds.400m</i>	-0.705	0.230	-1.154	-0.256	1.00	2
Wet.1200m	0.249	0.215	-0.096	0.841	0.59	1

Notes: Adjusted S.E. are listed for each estimate. Parameters with a negative influence are shown in italics. Parameter importance is calculated from the number of models and the weight of the models of the candidate set in which the parameter appears. Codes are given for forb abundance (Frb.Ab), site area (S.Area), habitat connectivity (dispersal potential (Flux.250m) and generalized betweenness centrality (BCIIC.250m)), the configuration of suitable habitats (Config.250m); and the percentage of cropland (Crops.250m), roads (Rds.400m), wetlands (Wet.800m) and woodlands (Wood.400m, Wood.800m, and Wood.1200m) in the surrounding landscape.

Table 4.10. Results of model selection for polylectic and oligolectic bees. The candidate set consists of all models within two AIC units of the top model for predicting the abundances of polylectic and oligolectic species.

Model (information criterion)	K^a	(Q)AICc ^b	$\Delta(Q)AICc^c$	wi^d
Polylectic bees (QAICc)				
Flux.800m + Frb.Ab	3	41.64	0.00	0.90
Oligolectic bees (AICc)				
S.LCTs + Dev.400m	3	34.97	0.00	0.39
NL.800m	2	35.40	0.43	0.32
<i>Null</i> (intercept only)	1	35.57	0.59	0.29

Notes: ^{a-d} K—The number of model parameters; AICc = Akaike's Information Criterion adjusted for small sample size or QAICc = quasi-AICc for overdispersed models; $\Delta(Q)AICc$ = relative (Q)AICc; wi = Akaike weight; Codes are given for the abundance of blooming forbs (Frb.Ab), habitat connectivity (dispersal potential (Flux) and number of links (NL), area of developed land cover (Dev), and site heterogeneity (S.LCTs) within each radial distance from a study site.

Table 4.11. Model-averaged coefficients importance of predictors of polylectic and oligolectic bee abundances. Estimates \pm standard error, confidence intervals, predictor importance and the number of models in which each parameter appears are listed.

Coefficients (model-averaged)		95% Confidence Interval			Parameter Importance	
Variable	Estimate	S.E.	lower	upper	Importance	N Models
Polylectic bees (QAICc)						
Flux.800m	0.323	0.089	0.301	0.392	0.96	1
Frb.Ab	0.450	0.096	0.403	0.533	0.93	1
Oligolectic bees (AICc)						
S.LCTs	0.257	0.321	0.066	1.388	0.39	1
Dev.400m	0.210	0.345	0.044	1.225	0.39	1
NL.800m	0.196	0.359	0.123	1.364	0.32	1

Notes: Adjusted S.E. are listed for each estimate. Parameter importance is calculated from the number of models and the weight of the models of the candidate set in which the parameter appears. Codes are given for the abundance of blooming forbs (Frb.Ab), habitat connectivity (dispersal potential (Flux) and number of links (NL) within to other habitat patches within 800m of a study site, the area of developed land cover within 400m of a study site, and site heterogeneity (S.LCTs).

Table 4.12. Results of model selection for bees with different foraging capacities. The candidate set consists of all models within two AIC units of the top model for predicting the abundances of species which forage within 250m, 400m, 800m, 1200m, and more than 1200m of the study site.

Model	K ^a	(Q)AICc ^b	Δ(Q)AICc ^c	wi ^d
Foraging capacity within 250m (AICc)				
Crops.250m + Wood.250m	3	26.51	0.00	0.91
Foraging capacity 250-400m (AICc)				
BCIIC.250m + Wood.400m	3	32.85	0.00	0.73
BCIIC.250m	2	34.87	2.00	0.27
Foraging capacity 400-800m (QAICc)				
BCIIC.800m + Crops.800m + Wood.400m	4	34.40	0.00	0.92
Foraging capacity 800-1200m (QAICc)				
S.Grass + Wood.800m	3	31.84	0.00	0.67
S.Grass	2	33.25	1.41	0.33
Foraging capacity greater than 1200m (AICc)				
Flux.1200m	2	24.99	0.00	0.49
S.Area	2	25.82	0.83	0.33
Crops.400m + Dev.800m	3	26.99	1.99	0.18

Notes: ^{a-d} K—The number of model parameters; AICc = Akaike's Information Criterion adjusted for small sample size or QAICc = quasi-AICc for overdispersed models; Δ(Q)AICc = relative (Q)AICc; wi = Akaike weight. Codes are given for the area of land cover types in the landscape surrounding a study site (cultivated (Crops), woodlands (Wood), and development (Dev)), habitat connectivity (generalized betweenness centrality (BCIIC) and dispersal potential (Flux)), within each radial distance of a site, as well as the area of a study site (S.Area) and the proportion of grass vegetation within each site (S.Grass).

Table 4.13. Model-averaged coefficients and importance of predictors of bee abundances within foraging groups. Estimates \pm standard error, confidence intervals, predictor importance and the number of models in which each parameter appears are listed for groups which forage within 250m, 400m, 800m, 1200m, and more than 1200m of the study site.

Coefficients (model-averaged)			95% Confidence Interval		Parameter Importance	
Variable	Estimate	S.E.	lower	upper	Importance	N Models
Foraging capacity within 250m (AICc)						
Crops.250m	0.758	0.347	0.324	1.347	0.91	1
Wood.250m	0.888	0.268	0.364	1.412	0.91	1
Foraging capacity 250-400m (AICc)						
BCIIC.250m	0.703	0.342	0.033	1.372	1.00	2
Wood.400m	0.513	0.416	0.062	1.337	0.73	1
Foraging capacity 400-800m (QAICc)						
BCIIC.800m	0.661	0.059	0.545	0.777	1.00	1
Crops.800m	0.626	0.046	0.536	0.716	1.00	1
Wood.400m	0.399	0.050	0.300	0.496	0.92	1
Foraging capacity 800-1200m (QAICc)						
Flux.400m	0.281	0.194	0.297	0.519	0.69	1
Foraging capacity greater than 1200m (AICc)						
Flux.1200m	0.697	0.268	0.171	1.223	0.49	1
S.Area	0.665	0.276	0.124	1.205	0.33	1
Crops.400m	0.521	0.267	-0.002	1.044	0.18	1
Dev.800m	-0.618	0.267	-1.141	-0.094	0.18	1

Notes: Adjusted S.E. are listed for each estimate. Importance is calculated from the number of models in the candidate set in which each parameter appears and the weights of those models. Codes are given for the area of land cover types in the landscape surrounding a study site (cultivated (Crops), woodlands (Wood), and development (Dev)), connectivity (generalized betweenness centrality (BCIIC) and dispersal potential (Flux)) within each radial distance of a site, as well as the area of a study site (S.Area), and the proportion of grassland cover within each site (S.Grass).

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CHAPTER 5: THRESHOLDS OF CULTIVATION AND FORAGE HABITAT FOR WILD BEES: THE DISTRIBUTION OF POLLINATION SERVICES ACROSS A PRAIRIE LANDSCAPE

ABSTRACT

Insect pollination is a critical ecosystem service in wild plant communities and is carried out primarily by wild bees. Widespread conversion of suitable habitats to agriculture and other land uses threatens the sustainability of pollination services as bee populations decline, but more studies are needed which assess the status of wild bees across entire landscapes. Here, I used a spatial habitat model, the InVEST pollination model of the Natural Capital Project ©, and land-cover data to estimate bee abundance for seven guilds based on sociality and nesting strategy. Distributions were mapped across an agriculturally-fragmented tallgrass prairie landscape to identify potential reservoirs or dearth of bees, differences in distribution among guilds, and potential thresholds of land conversion and suitable habitat that are able to support a diverse wild bee community. Overall, pollination services were most continuous for long-distance foragers (large, social, cavity-nesters and large wood-nesters) and most limited for small wood-nesters. The primary differences in landscape composition between areas of high and low bee abundance indices were the extent of suitable forage, which was greater in high abundance areas, and the percentage of croplands, which was higher in low abundance areas. Bee abundance indices increased with the proportion of land area with suitable forage cover until approximately 68%. The lower threshold was near 37% cover, after which abundance declines. Abundance indices were negatively correlated to crop cover and development, and the threshold established for the former was 16.7%, after

which abundance declined more sharply. Foraging bee abundance was positively correlated to woodland and road land cover types, particularly within areas where abundance indices were low. Importantly, the pollination model used here was a useful tool for identifying areas where conservation and restoration efforts may be most effective according to the underlying associations to resource availability. The study area examined here, the Southeast Prairies BUL, appears to be an oasis for wild bees in a landscape that's been highly modified by resource-poor row crop agriculture. This approach easily allows for future monitoring which helps track progress toward sustainable management of pollinator populations and habitats across large scales.

INTRODUCTION

Pollinators have an important ecological role in terrestrial ecosystems (Kearns et al. 1998) since pollination is an essential component in sustaining wild plant communities (Ashman et al. 2004; Aguilar et al. 2006). The loss of pollinator species which service keystone plant species in particular, has the potential to alter the structure of entire biotic communities via cascades of changes in species interactions (Allen-Wardell et al. 1998; Kearns et al. 1998). Although the pollination services of wild bees are primarily driven by the abundance of dominant species (Winfree et al. 2015), biodiversity loss is generally associated with reduced ecosystem functioning (Cardinale et al. 2012; Tilman et al. 2012). Because this association is not often tested in large, landscape-scale systems (Duffy 2009; Cardinale et al. 2012), and given the current rate of biodiversity loss (Pimm et al. 2014), it's important to better understand its role in sustaining ecosystem functions at larger scales. A recent study (Koh et al. 2016) on the status of pollination services across the coterminous United States identified widespread declines in wild bee abundances, with models indicating a 23% decline over a five-year period. These declines were primarily attributed to habitat conversion to row crops and average bee abundance was especially low for the Corn Belt area of the Great Plains (Koh et al. 2016), including Nebraska.

Although plant-pollinator networks are often asymmetric and nested (Bascompte et al. 2006), with high levels of redundancy (Memmott et al. 2004; Fortuna and Bascompte 2006) among generalists species which can sustain network structure under changing conditions, continued loss of not only species, but also their interactions

(Hegland and Totland 2008; Le Conte and Navaias 2008; Tylianakis et al. 2008) could ultimately lead to collapse of seemingly robust network structure (Memmott et al. 2004; Fortuna and Bascompte 2006). Therefore, evaluating pollinator response to environmental change and identifying drivers of species loss is an important component of conserving or restoring the level of pollination function required to maintain the plant communities of grasslands and other terrestrial ecosystems.

Landscape structures, both manmade and natural, can act as barriers to invertebrate dispersal among habitat patches. This includes forests (Cozzi et al. 2008), roadways (Koivula and Vermeulen 2005), rivers or other water bodies (Sciarretta and Trematerra 2006), as well as open fields or crop fields (Kumar and O'Donnell 2009). Highly mobile flying insects are thought to be less impeded by such elements (Driscoll and Weir 2005; Koivula et al. 2005) but barriers may be especially consequential for central place foragers, such as bees, which frequently travel between separate habitat patches for foraging and nesting. Many bee species are known to cross potential barriers between forage patches (Zurbuchen et al. 2010a), but often only do so when local floral resource availability declines (Bhattacharya et al. 2003; Kreyer et al. 2004). For some species (e.g. *Andrena*), only few individuals will cross even unpaved roads (Franzen et al. 2009). Still, that many bees hesitate, but ultimately will cross potential barriers to reach forage in response to resource availability demonstrates adaptive capacity in foraging behavior and may provide insight to resource use when quality forage habitat is sparsely distributed throughout a landscape.

Habitat loss, fragmentation and degradation have been deemed the primary culprits of pollinator decline in the past few decades of research (Ricketts et al. 2008). However, intermediate levels of habitat conversion, specifically development and agriculture, have sometimes been associated with positive effects on bee abundance and species richness (Winfree et al. 2007), possibly by promoting resource availability within small but numerous partial habitat types (Cane et al. 2006; Winfree et al. 2008), which offer complementary nesting and forage resources (Westrich 1996; Farhig 2003). Not only are bees highly mobile, but they are also adapted to utilizing resources with patchy distributions, which likely contributes to tolerance of moderate disturbance (Carré et al. 2009) and habitat loss (Winfree et al. 2009). Importantly, species responses have been shown to vary among guilds and foraging capacities (Steffan-Dewenter et al. 2006) and are often associated with the quality of the matrix which surrounds habitat fragments (Westrich 1996). Thus, identifying thresholds of land use change or suitable quality habitat area at which bees respond, positively or negatively, deepens our understanding of pollinator-environment interactions and provides valuable information to guide conservation efforts for pollinating organisms and their services.

The objectives of this study were to 1) estimate, map, and compare the abundance distributions of wild bees according to sociality and nesting strategy across a tallgrass prairie landscape in relation to the distribution of nesting and forage habitats for different guilds, 2) identify patterns of consistently high and low estimates of bee abundance within the study area and the broader landscape, 3) determine whether these patterns correlate to differences in landscape composition, and 4) identify the thresholds of

relevant land cover types at which changes in bee response occur. A modeling approach was employed which uses land cover data and considers differences among species in resource requirements and foraging capacity. Such tools are valuable in that reasonable estimates of bee distributions can be obtained without necessarily detailed knowledge of species assemblages or abundances, and areas where conservation efforts could bolster the supply of pollination services can be identified for further study of how modeled distributions reflect the actual distribution of wild bees.

METHODS

In this study I used the InVEST pollination model (Lonsdorf et al. 2009) of the Natural Capital Project © to estimate and map the abundance distributions of wild bees across a landscape and to predict potential reserves and deficits of pollinators and their services. Species were categorized by characteristics of sociality, nesting strategy, and foraging capacity, resulting in seven guilds (Table 5.1) for which abundance data from field collections was compared to modeled predictions of abundance. The pollination model is calibrated by each guild's foraging capacity to calculate an abundance index for each parcel of land in a geographic information system (GIS) for which land cover data and habitat suitability information is provided. Bees were sampled from June to August of 2012 and 2014.

Study area

The study location consisted of an agricultural landscape in southeastern Nebraska, with specific study sites in Johnson, Pawnee, and Richardson Counties. All sites were located within an area designated by the Nebraska Natural Legacy Project as a

Biologically Unique Landscape (BUL), this one being the Southeast Prairies BUL. A total of 15 sites were selected from three of the dominant grassland types in the landscape: remnant tallgrass prairie (also referred to as haymeadow), grazed pasture, and properties enrolled in the USDA Conservation Reserve Program (CRP). Five privately owned properties were selected for each grassland type based on management practices and landowner permission. The remnant prairies were managed for hay production, with haying occurring once per year. The grazed pastures were actively grazed by cattle during the study, although cattle were rotated at different times. The CRP properties were all CP25 grass/forb seed mixes at least five years into their CRP contract. These natural and semi-natural grassland patches were selected as representatives of different suitable bee habitat types within a mosaic of row crop agriculture (predominantly corn or soybeans), woodlands, and grasslands. Study sites were each sampled twice in June, July, and August of 2012, and at least once in each of the same months in 2014 with the exception of two CRP sites that had been converted back to crop production after the first year of the study and were therefore not available for further sampling. Study sites ranged in size between 3.1-23.6 hectares and the focal study area was concentrated within the north-central third of the BUL.

Bee sampling and identification

The wild bee communities of the 15 grassland sites were sampled with blue vane traps (SpringStar® Inc., Woodinville, WA, USA) suspended from a PVC pole at the level of the surrounding vegetation. Traps were set up for 48 hours during appropriate weather conditions (avoiding high winds and rain), with four traps assigned to each study site. At

the end of each sampling session, the contents of each trap were transferred to Ziploc® freezer bags in the field, then placed in a freezer until specimens could be sorted and identified. Bees were identified to species when possible but some groups, such as *Lasioglossum*, were identified to morphospecies. Bees were first identified to genus using Michener et al.'s Bee Genera of North and Central America (1994) and then to species using a combination of keys on discoverlife.org, local keys to prairie bees of Missouri and a reference collection with confirmed species identifications that was created with professional assistance from Mike Arduser at the Missouri Department of Conservation, St. Louis Regional Office, St. Charles, MO, 63304 USA. Information on bee functional traits was obtained from the same resources.

Classification of bee species into functional guilds

Species were categorized into guilds based on sociality, nesting strategy, and foraging capacity (Table 5.1). Only eusocial species with a queen as the only egg-laying female and workers performing other tasks were considered *social*. These were further categorized as *large* (*Bombus* spp.) or *small social* (*Halictus* spp.) species. Nesting strategies included *cavity-nesters*, *ground-nesters*, and *wood-nesters*. *Cavity-nesting* species are hypergeic (above-ground; Oertli et al. 2005) and nest in existing natural cavities (Michener 2007). Large social species were the only cavity-nesters. *Ground-nesting* species are endogeic (below-ground; Oertli et al. 2005) and excavate nests in the soil. Small social species were ground-nesters, and solitary species were further categorized as medium-large and small ground-nesting guilds (size ranges described below). *Wood-nesting* species are hypergeic and use wood or twigs to construct their

nests. Wood-nesters were additionally categorized as *large* (*Xylocopa virginica*), *medium*, and *small* size ranges (see below).

A foraging distance, in meters, is required to calibrate the InVEST pollination model for each guild. Foraging capacities were estimated from published experiments in which species body sizes were reported (i.e. summaries provided by Gathmann and Tscharntke 2002 and Zurbuchen et al. 2010b). Extreme distances from homing experiments on large species within *Bombus* and *Xylocopa* were excluded, as were values which fell well outside the range of relevant foraging scales as described by Gathmann and Tscharntke (2002). The latter were broad categories used by Le Féon et al. (2013) with maximum foraging distances for small, medium, and large species corresponding, approximately, to 400, 800, and 1200 meters, respectively, from the nest site. Remaining distances reported for relevant species were averaged for different size ranges: within 6-11mm and 11-13mm for small and medium-large ground nesters, respectively, and within 5-9.5mm and 10-13.5mm for small and medium wood nesters, respectively. Foraging capacity of *Bombus*, social Halictids, and *Xylocopa* were not estimated by body size, but rather by non-homing distances summarized within Zurbuchen et al. (2010b), which were averaged among the species or reports of each genus. As with the field data, *Bombus* species represented large social species, and social sweat bees represented small social species. *Xylocopa virginica* was the only representative species of large wood nesters in field data. A single specimen of *Megachile sculpturalis*, another large wood-nesting species, was collected but excluded as both a singleton and an exotic. *Apis mellifera*, another cavity nester, was also not considered, neither for estimating guild foraging

capacities nor for field data from the 15 sampled study sites within the Southeast Prairies BUL, despite its well documented foraging capacity. All cleptoparasitic species and males were excluded since they don't engage in nest-building or act as typical central place foragers.

Land cover and habitat suitability classification

Land use and land cover (LULC) data for the area were obtained to identify potential nesting and forage habitat across the landscape and construct distribution maps for wild bees accordingly in a geographic information system (GIS) using ArcGIS® software and ArcMap10™. The LULC map was created from data with 30-meter resolution obtained from the Rainwater Basin Joint Ventures project (2012), supplemented with land cover data specifically for the Southeast Prairies BUL (Nebraska Natural Heritage Program and Northern Prairies Land Trust). The data was updated, where necessary, with surveys within 1200m of each study site during 2013 and 2014. Land cover types from all sources were categorized into seven broad categories: grasslands, woodlands, croplands, development, roads, other uncultivated, and resourceless. The cover types within each classification were assigned a score (0-1) for availability of nesting and forage resources (Table 5.2). Scores were adapted from those given for the pollination model of ESTIMAP (Zulian et al. 2013), a means of assessing ecosystem services on a regional scale in Europe, as well as scores from a recent study by Koh et al. (2016) in which expert opinion on seasonal differences of the suitability of different land cover types for cavity-, wood-, stem-, and ground-nesting guilds was used in an evaluation of the status of pollination services across the United States. When

multiple potential suitability scores were available, selection of the most appropriate score was based on land cover quality within a tallgrass prairie context as assessed by Hines and Hendrix (2005).

Suitability scores for marginal roadside habitat were only given for the ESTIMAP model, which were not differentiated among nesting guilds. Also, Zulian and colleagues explicitly state that higher nesting and forage scores were assumed due to the manner in which roadway data was extracted from the land cover dataset prior to modeling. Therefore, the scores used here are based on ESTIMAP scores for each of the relevant roadway categories in terms of rank, but were adjusted to more closely reflect the scores given by Koh and colleagues by averaging the scores given by the latter for the more intensely managed grasslands and low level development (e.g. “other hay” and “open space”, respectively) in order to mimic the mowing of larger roadsides and provide scores which were reasonably differentiated between nesting guilds. Additionally, Hines and Hendrix (2005) considered row crops as resourceless land cover and Zulian *et al.* (2013) considered corn, specifically, to be of no forage value. However, it was assumed that marginal forage (e.g. weedy species) and marginal nesting would be available on the edges of the crop fields and so, the lower scores derived by Koh *et al.* (2016) were selected.

Predicting bee abundance and pollination services

Bee abundance was modeled for the landscape using InVEST software (Lonsdorf *et al.* 2009) developed within the Natural Capital Project ©. The InVEST pollination model uses data on nesting and forage resources in conjunction with foraging data for bee

species or guilds to generate estimates of foraging bee abundance on a given parcel of land as a proxy of pollination services. The first step of modeling creates a “source map” of nesting bee abundance indices. Then, based on these distributions, the pattern of forage habitat, and the foraging capacities of the nesting bees, a “pollinator services map” is created from proximity-weighted averages of bee abundance within the foraging distance of each modeled guild. What is mapped represents the relative abundance of foraging bees (visiting bees) likely to travel to a given parcel of land from the surrounding nesting habitat within the limits of each guild’s foraging capacity. This estimate is reported as an index of pollination services.

Pollinator supply was calculated first, using nesting and forage data for each cell of a land cover map (Figure 5.1) to estimate nesting bee abundance (P) for each guild (β) within cell x :

$$P_{x\beta} = N_j \frac{\sum_{m=1}^M F_{jm} e^{\frac{-D_{mx}}{\alpha\beta}}}{\sum_{m=1}^M e^{\frac{-D_{mx}}{\alpha\beta}}}$$

which accounts for the nesting suitability (N) of each land cover type (j) and forage quality (F) within the relevant foraging range of each guild ($\alpha\beta$) considering the Euclidean distance (D_{mx}) between cells m and x in the landscape (Greenleaf et al. 2007). This provides an abundance index for each guild of wild bees nesting within each cell, and a potential for pollination services. Since the service is provided during foraging, the second step is to estimate the abundance of bees that visit cells with suitable forage land cover types, using the forage component of the previous equation as follows:

$$P_{ox\beta} = \frac{P_{x\beta} e^{\frac{-D_{ox}}{\alpha\beta}}}{\sum_{x=1}^M e^{\frac{-D_{ox}}{\alpha\beta}}}$$

where bees of guild β travel from source cell x to forage in cell o and $D_{ox\beta}$ is the distance between these cells. In this equation, the numerator normalizes the contribution of foraging bees by the relevant foraging area (i.e. within the foraging distance of each guild; Winfree et al. 2005), and is the distance-weighted proportion of bees visiting cell o from cell m to forage. The InVEST pollination model is designed to assess crop pollination potential for specified agricultural parcels with an estimated demand for services to achieve sufficient yields. However, when agricultural areas and pollination demands are not specified, a visitation estimate is provided for each cell in the landscape. Here, the visitation output for the cells that comprise each study site were averaged to get an estimate of foraging bees on these parcels. These values were then compared to actual abundance data for each site. Study sites were not designated as farm parcels (i.e. specified land classification to which a pollination demand can be assigned) because doing so would not capture the variation in nesting or forage suitability within sites. The full model is designed to estimate pollination services on designated farm parcels which are presumably homogenous.

Correlation of predicted bee abundance to landscape composition

The distribution of each of the seven guilds across the landscape was assessed by comparing heatmaps of guild indices and was used to identify areas of consistently high or low relative abundance beyond the focal study area. A total of 24 pockets of consistently high abundance indices were identified as hotspots and 31 pockets were

consistently cool, with low average foraging indices. The extent of land area covered by seven broad cover categories (i.e. crops, suitable forage, woodlands, roadways, development, uncultivated areas, and resourceless) was quantified as a proportion (percent composition) within each area of interest and was used in correlations with the average foraging index for all combined guilds. Spearman rank correlations were used when data failed Shapiro-Wilk normality tests, and Pearson product moment correlations were used for normally distributed values. Differences in average foraging indices between areas of high and low abundance within each land cover category were determined using a multiple response permutation procedure in PC-ORD (PC-ORD version 6, MjM Software, Glenden Beach, OR, USA).

Thresholds of land cover which influence bee distributions

Finally, the average foraging abundance index across all guilds was also used for determining the threshold values of the land covers which differed in land area between high and low abundance areas. The potential for multiple threshold proportions of land area was initially explored using breakpoint analysis in R via the packages “ggplot2” and “segmented” (R Core Team 2013). Then, two-segmented piecewise regressions were built around the best breakpoints, with proportion land cover as the independent variable and average foraging index as the response variable using SigmaPlot 13 (Systat Software, San José, CA). These breakpoints were used to indicate the threshold proportion of land cover at which predicted bee response changed, with abundance indices declining sharply, increasing suddenly, or leveling off.

RESULTS

A total of 8,016 individuals were collected from the 15 study sites of the Southeast Prairies Biologically Unique Landscape, of which 21 genera and 48 species were used as representatives in the InVEST pollination model in this context (Table 5.1). Seven species of bumble bees (*Bombus*) represented large social cavity-nesting species and two species, *Halictus ligatus* and *H. parallelus* were representative of small social species. Medium to large solitary ground-nesters consisted of 15 species of the genera *Anthophora*, *Melissodes*, *Svastra*, and *Xenoglossa*, and small ground-nesters included 12 species from seven genera. A single species, *Xylocopa virginica*, was used to represent large wood-nesters. Medium wood-nesters were represented by five species of *Megachile*. Each of the six genera included in the small wood-nesting guild were represented by single species.

Distribution of bee abundances among functional guilds

Generally, abundance distributions among guilds were consistent between predicted and observed relative abundances, with highest numbers belonging to solitary ground-nesting and social guilds (Figure 5.2). Collectively, solitary ground-nesters were the majority of observations, followed by large social species and wood-nesters for most study sites (Figure 5.2a). Exceptions included the sites CL and LV, where large social species comprised only 6.7% ($\pm 2.5\%$) and 8.7% ($\pm 4.3\%$), respectively, and were nearly equal to or surpassed in abundance by wood-nesters. The relative abundance of small social species was more consistent across study sites, ranging between 3.1% and 7.5%.

The distributions of foraging bees within each guild predicted by the InVEST pollination model were less variable between sites than observed abundances per guild (Figure 5.2b). Large social bees were expected to be least represented in sites CC and CL (foraging bee abundance indices were 0.294 ± 0.0001 and 0.292 ± 0.0001 , respectively) and most in sites WA and WE (0.421 ± 0.0002 and 0.420 ± 0.0002 , respectively). Small social species were predicted in higher relative abundances than what were observed at all sites, with estimates ranging between 0.295 ± 0.0165 (for site LV) and 0.470 ± 0.0008 (for site LH).

Predictions and observations of large wood-nesting bee abundance were closest for sites with the highest abundances (BE: $16.3\% \pm 0.01\%$ and $12.3\% \pm 2.1\%$, respectively; CL: $16.7\% \pm 0.01\%$ and $11.6\% \pm 4.1\%$, respectively), but the greatest differences were 11.4% and 12.1% for WA and WE, respectively, where relative abundances of only 0.052 ± 0.041 and 0.025 ± 0.016 were observed. Greater relative abundances were predicted for medium and small wood-nesting bees than what were observed, and differences were largest for these groups. Medium wood-nesters differed by 18.8% (0.013 ± 0.008 observed) and 20.2% for HE and KH, respectively, where relative abundances of 0.013 ± 0.008 and 0.023 ± 0.009 were observed, and small wood-nesters differed by 20.8% and 22.6% for HE and CS, respectively, where relative abundances of only 0.0022 ± 0.002 and 0.022 ± 0.020 were observed.

Modeled distribution of social bees

The distribution of social species among study sites as predicted by the InVEST pollination model were generally high, with hot colors dominating the focal study area

for both supply (i.e. nesting; Figure 5.3a and c) and service (i.e. foraging; Figure 5.3b and d) indices. The three easternmost sites were expected to have lower abundances of visiting bees, with a higher density of adjacent low abundance patches, and this difference is more apparent for small social species than large when comparing the relative abundances of foraging bees (Figures 5.3b and d). These guilds have different nesting strategies, and the pockets of low supply indices are more pronounced for large social species (Figure 5.3a) than small social species (Figure 5.3c).

In the broader landscape, distribution of large social species is most densely concentrated in the central portion of the BUL for both nesting (Figure 5.4a) and foraging indices (Figure 5.4b). Small social species are more evenly distributed across the BUL, but both nesting (Figure 5.4c) and foraging indices (Figure 5.4d) were highest in the north-central portion. Maximum predictions of nesting bees were similar for both social guilds, with 0.678 and 0.663 for large and small social bees, respectively, while predicted foraging indices were greater for small social bees, with maximum values at 0.514 versus 0.423 for large social bees (Table 5.3).

Modeled distribution of solitary ground-nesting bees

The predicted abundances of large and small solitary ground-nesting species were similar, with high and low abundances generally expected at the same sites for nesting (Figure 5.5a and c) and foraging indices (Figure 5.5b and d). Across the landscape, small and large solitary ground-nesters are similarly distributed, with larger species showing slightly higher relative abundances, especially for foraging bees (Figure 5.6a and b), whereas small species are expected to nest and forage in lower abundances (Figure 5.6c

and d) but with similar distribution as large ground-nesters. Although the expected maximum relative abundances of large species were greater for both nesting and foraging indices than small species (nesting: 0.687 vs. 0.555, foraging: 0.735 vs. 0.662, respectively), the means were very similar for all solitary ground-nesters (Table 5.3; MG—nesting: 0.253 ± 0.168 , foraging: 0.262 ± 0.183 ; SG—nesting: 0.250 ± 0.114 , foraging: 0.260 ± 0.130).

Modeled distribution of solitary wood-nesting bees

Some of the largest within-guild differences in predicted abundance indices were among solitary wood-nesting species. Nesting indices were lower for all three categories of wood-nesters than social species or solitary ground-nesting species among study sites, and were largely restricted to wooded areas (Figure 5.7a, c, and e). The predicted services of wood-nesting bees were greatest for large species, with hot colors covering the area where study sites were concentrated (Figure 5.7b) whereas hot spots are gradually condensed around wooded areas as wood-nesting species decrease in body size (Figure 5.7d and f).

In the broader context of the Southeast Prairies landscape the nesting indices are similar among all sizes of solitary wood-nesting bees and are concentrated within wooded areas, while obvious differences are seen for the foraging index among large, medium and small species (Figure 5.8). Like large social species, the services of large wood-nesters are broadly distributed across the BUL but are concentrated within the central portion, especially in the focal study area (Figure 5.8b). Pockets of low relative abundance appear in the map for medium species, with areas of high foraging index

values retained within the central portion of BUL, including the focal study area where bees were sampled (Figure 5.8d). These hotspots are less pronounced for small species and extend little beyond the areas with high nesting indices (Figure 5.18e and d).

Although the mean foraging indices for wood-nesting species (LW- 0.081 ± 0.039 , MW- 0.094 ± 0.051 , and SW- 0.100 ± 0.075) were lower than that of social and ground-nesting species, the maximum relative abundances predicted for nesting bees were greater for medium and small wood-nesters considerably higher than that of large species (Table 5.3; MW = 0.813, SW = 0.888). Mean nesting indices, however, were also lowest among the guilds examined here (Table 5.3; LW: 0.087 ± 0.145 , MW: 0.095 ± 0.155 , SW: 0.099 ± 0.156).

Land cover composition for areas of high and low abundance indices

Several areas across the landscape show consistently high or low supply and service indices. These are shown as repetitive hot or cool pockets in the previous maps and are more specifically identified from a map of average foraging indices across all social and solitary guilds (Figure 5.9a). These areas of interest include the focal study area (FA) in the central portion of the landscape and the western edge of the BUL (W1) as areas of high abundance. The areas of consistently low abundance were pockets to the southwest (C1 and C6), east and southeast (C2, C3, and C5), and north (C4) of the focal study area, as well as the area outside the BUL which borders the western edge (W2). Total area of high (yellow to red) and low (green to blue) were also compared (SP and NP, respectively).

The primary differences between hot and cool spots across the landscape were the proportions of cultivated and suitable forage (i.e. grassland) land covers. Fallow and otherwise uncultivated land, as well as roads, development, and resourceless land covers occurred in similar proportions among all areas of interest, ranging between 0% and 7% land area (Figure 5.9b). For the total area of high relative bee abundance (SP), crops comprised 12.7% of land area, forage 67.9%, and woodlands 14.6%, whereas the total area of low relative abundance (NP) consisted of 50.9% crops, 33.6% forage, and 9.3% woodlands. Along the west edge of the BUL, the lower abundance area (W2) was composed of 51.9% crops, 35.9% forage, and 9.3% woodlands compared to 12.1% crops, 69.7% forage, and 13.7% woodlands for the adjacent high abundance area (W1).

Finally, within the designated BUL, the focal study area (FA) was composed of 14.5% crops, compared to 43.1% and 37.2% in the nearest pockets to the southwest (C1) and along the eastern side of the focal area (C2), respectively (Figure 5.9b). The focal area was also comprised of 65.7% forage and 14.9% woodlands compared to 49.3% forage and 2.1% woodlands in the adjacent pocket (C1) and 37.4% forage on the eastern side (C2), although woodlands covered a similar proportion of land with 13.8%. The east (C3) and southeast (C5) pockets of low relative bee abundances also had similar proportions of woodlands as areas of high relative abundances, with 10.3% and 14.3%, respectively, while the north pocket (C4) and southwest pocket (C6) had lower proportions of woodlands (6.3% and 7.3%, respectively). The proportion of forage cover in these remaining pockets was lowest in C3, with 25.3%, followed by the nearby C6 with 38.1%. C3 also had the greatest amount of cultivated land cover, with 55.2%. C4

and C6 were covered by 40.2% and 49.4% forage, and 47.1% and 37.4% crops, respectively. Nearly equal portions of land area were covered by crops and forage habitat in the C5 area, with 40.6% and 38.1%, respectively.

Correlations of land cover composition to predicted bee abundances

In Spearman rank and Pearson product moment correlations the extent of crop and forage cover in the landscape were consistently most strongly correlated to predicted abundances of foraging wild bees, especially within patches where low bee abundances were predicted, although the extent of development, roads, and woodlands were also important in certain areas of interest (Table 5.4). Predicted relative abundances tend to decrease with increasing area of cropland within areas of low abundance, both when considering the average of all combined low abundance areas ($r = -0.345$, $p = 0.043$) and the mean abundance predicted for crop patches alone ($r = -0.392$, $p = 0.026$), but this is not a significant correlation after Bonferroni corrections (adjusted significance is 0.007). The same pattern was found when areas of high and low abundances were combined, but with greater strength (total area: $r = -0.718$, $p < 0.001$; within crop patches: $r = -0.503$, $p < 0.001$, $n = 57$). The area of suitable forage cover was positively correlated to predicted wild bee abundance within low abundance areas ($r = 0.557$, $p = 0.001$), but had a much weaker correlation within high abundance areas ($r = 0.212$, $p = 0.310$). The strongest correlation was for combined high and low abundance areas using the average abundance scores within suitable forage patches ($r = 0.736$, $p < 0.001$).

Woodlands were also positively correlated to predicted relative bee abundance in low abundance areas, but only when total mean abundance was considered (Table 5.4: $r =$

0.397, $p = 0.027$), and not for predicted abundances within woodland patches alone ($r = 0.268$, $p = 0.144$). However, neither correlation was significant following Bonferroni corrections with adjusted significance of 0.007. Relative abundance indices tend to increase with area of road cover both within low abundance areas (NP: $r = 0.586$, $p = 0.007$), and overall (SP and NP combined: $r = 0.509$, $p = 0.001$), but only for predicted abundance of bees seeking forage within patches of road cover. The proportion of developed land (both rural and urban or suburban development types) were negatively correlated to bee abundance when the total area of combined hotspots and cool-spots was considered ($r = -0.301$, $p = 0.036$), but not significantly after Bonferroni corrections. The extent of uncultivated and resourceless land cover types were only weakly, and inconsistently, correlated to foraging bee abundance indices, with only correlations of resourceless areas (i.e. waterways and bodies) approaching significance (SP: $r = 0.440$, $p = 0.59$; NP: $r = -0.356$, $p = 0.056$).

Comparisons of service indices within land cover types between areas of high (SP) and low (NP) abundance revealed differences in predicted distributions of foraging bees among crops, woodlands, and roads (Table 5.5). More bees are expected to search for forage among croplands ($A = 0.0968$, $p = 0.0001$) in low abundance areas than high abundance areas and greater abundances are expected among woodlands ($A = 0.0818$, $p = 0.0005$) and roadways ($A = 0.2648$, $p < 0.0001$) in high abundance areas than low abundance areas. As expected, the highest indices of foraging bees were estimated for suitable forage habitats and these values were comparable between areas of high and low

abundance ($A = 0.0035$, $p = 0.2780$), as were foraging indices for developed patches ($A = -0.0125$, $p = 0.9130$).

Thresholds of dominant land cover types

Finally, two- and three-segmented piecewise regressions identified the threshold proportions of land area covered by crops, suitable forage, and woodlands at which the rate of increase or decrease in predicted abundances changed (Figure 5.10). A single breakpoint was identified in a two-segmented piecewise regression on foraging bee abundance and crop cover at 16.7% ($\pm 9.27\%$), after which predicted foraging bee abundances decline (Figure 5.10a; $r^2 = 0.561$, $F_{3,52} = 24.421$, $p < 0.0001$). Upper and lower thresholds were identified for suitable forage and woodland area in three-segmented piecewise regressions. The increase in bee abundance peaks at 68.3% ($\pm 5.16\%$) of land area with suitable forage, and 37% ($\pm 2.29\%$) marks the lower threshold (Figure 5.10b; $r^2 = 0.579$, $F_{5,51} = 15.622$, $p < 0.0001$). The array was ill-conditioned on the final iteration of the initial regression of woodland cover. Although the ultimate outcome did not change, an outlier (H5) was removed to improve the fit and achieve normality. The greatest increase in predicted foraging bee abundances occurs between $12.1 \pm 3.9\%$ and $22.4 \pm 2.47\%$ woodland cover (Figure 5.10c) but the regression was not significant and adjusted R^2 was low ($r^2 = 0.101$, $F_{5,50} = 1.126$, $p = 0.359$). Therefore, both the upper and lower thresholds of woodland area are not strongly supported in this context. However, a further examination of the role of woodlands in the flow of pollen in the Southeast Prairies landscape is given in Appendix O in the form of a correlation

analysis between pollen-bearing bee species and the extent of woodland cover in the surrounding landscape.

DISCUSSION

The mapped index of bee abundance in this study clearly shows the lowest expected bee abundances in areas with the highest levels of agriculture, which reflects the consensus of experts that intensive agricultural landscapes are poorly suited for sustaining populations of wild bees (Hendrickx et al. 2007; Le Feón et al. 2010). Similar findings were reported in a recent nation-wide assessment of pollination services, which identified the Corn Belt, including Nebraska, as an area of decline (Koh et al. 2016). This study supplements that assessment by providing further evidence of these trends on a finer scale. In addition to the habitat fragmentation that accompanies land conversion to agriculture, wild bees are further subjugated to the effects of pesticide exposure and reduced floral availability. Hladik et al. (2016), for example, detected traces of 19 different pesticides in wild bees foraging in agricultural landscapes, many of which impair navigation ability at sublethal levels, as well as immunity and reproduction (Chmiel et al. 2010). Fortunately, however, the Southeast Prairies Biologically Unique Landscape in its current condition may be an oasis for bees within this portion of the former tallgrass prairie. Surrounding areas have been largely converted to row crops, primarily corn. Increasing land conversion to corn, specifically, was associated with declining bee abundance by Koh and colleagues (2016), who also note that bee abundance tends to increase with habitat restoration or enhancement, such as the

Conservation Reserve Program (CRP). These types of grasslands are among the dominant semi-natural habitats within the Southeast Prairies and although the correlation of predicted bee abundances and different kinds of grasslands was not directly tested or modeled in this study, it is plausible that such habitat restoration efforts contribute to the persistence of the bee community, in addition to the lower proportion of land area with crop cover within the boundaries of the BUL. Further research which examines habitat quality on a finer scale such as this would help delineate the contribution of specific land-use and land cover types to bee abundance within this context.

This study also demonstrates a useful tool for predicting bee abundances which can then be examined as a response to changes in landscape composition and resource availability without necessarily requiring extensive sampling of wild bees on a large scale. However, several limitations of the InVEST pollination model are explicit; two among these are relevant to this study and may have influenced the accuracy of its predictions of pollination services in this landscape. First, the size of suitable habitat patches is not considered in either of the model equations used here. Although bees can persist on fairly small patches of suitable habitat (Ricketts 2004), small patches may also support fewer species than large patches (Kremen et al. 2004). Therefore, the fine-scale differences of patch quality may not have been fully captured here and may be reflected in the discrepancies between the predicted abundance indices and the observed relative abundances from the focal study area. Second, the dynamics of foraging and nesting within even finer-scale features of a landscape than the habitat patch may also not be entirely captured by this model. Even with 30-meter resolution, nesting sites and small

foraging patches, such as a tree hollow or narrow roadside, will not be detected within 30 x 30 m pixels. Here, the marginal habitat patches offered by roadsides and the edges of crop fields were assumed and accounted for by the resource scores assigned to these land cover types. Although neither was specifically delineated within the LULC map, model performance was satisfactory and such software tools as this can be valuable for large-scale assessments in which management priorities must be set for habitat restoration or enhancement efforts.

The distribution of foraging bee abundance among the different guilds examined here largely corresponds to expectations. In terms of functional composition, most solitary bee species are ground-nesters and so this group naturally contributes substantially to the landscape's population and species pool, while fewer (about 30%) are wood- or twig-nesters (Mader et al. 2011). This was also predicted by the spatial habitat model in this study, with ground-nesters collectively comprising the majority and wood-nesting guilds comprising the smallest portion (Figure 5.1b).

Distribution of foraging bees across the landscape also largely corresponds to expectations based on foraging capacity and the observed behaviors of certain groups. Because foraging capacity is directly related to body size (Gathmann and Tscharncke 2002; Greenleaf et al. 2007), large, long-distance flying bees are expected to move more easily among habitats in a fragmented, heterogeneous landscape (Beil et al. 2008; Steffan-Dewenter et al. 2006) than small, short-distance flying bees (Gathmann and Tscharncke 2002; Zurbuchen et al. 2010b). Although movements are not always accurately predicted (Zurbuchen et al. 2010c), the range of body sizes used here to

calibrate the model, with large bees being > 10 mm and small bees being 6-10 mm, follows Gathmann and Tscharrntke (2002), Greenleaf et al. (2007), and Zurbuchen et al. (2010b). Short-distance flyers (150-600 m (Gathmann and Tscharrntke 2002; Zurbuchen et al. 2010b)) are expected to be more patchily distributed across the landscape than the large species, particularly bumble bees (*Bombus* spp.) and the eastern carpenter bee (*Xylocopa virginica*), for which high foraging bee abundances were expected across the BUL.

Some research suggests that bumble bees may prefer to forage at longer distances from the nest (Osborne et al. 1999; Dramstad et al. 2003), and they exhibit flexibility in foraging activity in response to forage quality by traveling farther distances for higher quality forage (Jha and Kremen 2013a). In contrast, large solitary bees (anthophorine bees within *Eucerini* and *Anthophorini* (Apidae) of body lengths > 12 mm) exhibit high site fidelity and floral constancy which result in conservative movement patterns with relatively short traveling distances (< 400 m) by individuals that do leave to other fragments (Dorchin et al. 2012). Although these groups have different nesting requirements, patterns in abundance distributions across the landscape largely reflect differences in foraging capacity. Small social species and large solitary ground-nesters are similarly distributed, as are smaller members of ground- and wood-nesting guilds. Those with the largest foraging capacities, the large social cavity-nesters and large wood-nesters, have more similar distributions than either has to smaller members of their guilds. In other work, large social bees are essential providers of pollination services in a fragmented landscape because of their flexibility in foraging behavior between high

quality fragments (Jha and Kremen 2013a) and these bees may behave similarly in the Southeast Prairies landscape.

The underlying mechanisms of bee decline are multifaceted and context-specific, but in a meta-analysis of bee responses to environmental change, Winfree et al. (2009) report that the only kinds of disturbance that were consistently associated with negative bee response across studies were habitat loss and fragmentation. Importantly, bee abundance and species richness were only significantly reduced in areas with little remaining natural habitat (Winfree et al. 2009). Here, within areas of high abundance, the proportion of land area with any kind of cover, including development and cropland, had little influence on foraging bee abundances. In contrast, in areas of low of consistently low bee abundance, indices not only decreased with increasing land area in crop cover, but increased with greater area of forage, woodlands, and roadways. This would imply both the importance of habitat heterogeneity to support the wild bee community and the potential for increased use of marginal habitat in areas where suitable habitat is sparse.

In a simulation study in which the marginal habitats of Voronoi-like randomized landscapes were manipulated, Rands and Whitney (2011) modeled bee abundances and concluded that increasing the widths and number of field margins would increase forage availability for all but the shortest-distance foragers (less than 125 meters). The capacity of the latter to sufficiently provision brood has been shown to decline with increasing distance to forage resources (Zurbuchen et al. 2010b). Importantly, such species may be numerous and comprise the bulk of certain pollinator communities, in which case special

habitat improvement methods may be needed (Zurbuchen et al. 2010c). For species which forage at greater distances, even marginal patches are more accessible (Osborne et al. 1999; Bäckman and Tiainen 2002). Bumble bees, for example, although preferring herbaceous forage in unfragmented species-rich grasslands (Carvell 2002), are known to exploit forage within small semi-natural patches of habitat along field margins and green lanes (Croxtton et al. 2002) within fragmented landscapes. Additionally, Carvell et al. (2004) found that bumble bee abundance and species richness is much greater within crop field margins in arable landscapes when these patches are subjected to habitat improvement, particularly by sowing a mix of wildflowers and grasses. Similarly, Hannon and Sisk (2009) found that enhancing marginal areas of agricultural fields with hedgerows supports a similar suite of wild bee species as woodlands, including certain otherwise uncommon species which are attracted to the intermediate composition of floral resources. Hedgerows also elicit a directional response in bumble bees, increasing the connectedness of habitat patches by encouraging movements along the hedgerow with significant effects on plant reproductive success (Cranmer et al. 2012).

Just as the margins of crop fields enhanced with wildflowers are beneficial to flower-visitors in agriculturally intensive landscapes (Feber et al. 1996; Pywell et al. 2005), roadsides can be improved by seeding with natural vegetation (Forman et al. 2003). Unlike field margins, however, roadsides are unplowed and may therefore offer better nesting resources for ground-nesting bees, which suffer reduced survival when nesting within fields due to annual tilling (Delaplane and Mayer 2000). Roadside habitats may be especially beneficial by providing connective corridors to other

fragments of suitable habitat (Forman et al. 2003; Croxton et al. 2005). Hopwood (2008), for example, found that the floral diversity, floral species richness, and the percentage of bare ground within roadside prairie restorations were positively associated with bee abundance and species richness, and that exposed soil accounted for 31% of variation in ground-nesting bee abundance. In this study, although the average foraging bee indices were higher for roadways in areas of high abundance, predicted abundance was positively correlated to the proportion of land area with roadway cover only within areas of low abundance. This marginal habitat may become a valuable resource for both foraging and nesting bees when suitable natural habitat is sparsely distributed across the landscape.

Although no critical threshold of woodland cover was established for this study, the proximity of woodlands have had an influential role in the level of pollination services provided by wild bees in other work on the subject. In a recent examination of pollination services to apple orchards, Joshi et al. (2016) reported greater visitation rates when unmanaged habitats, particularly forests, were within 250-500 meters of the orchard. The authors observed this for feral honey bees and solitary bees, but noted that these correlations were especially strong for *Bombus* species due to these areas having greater resources required by these bees. Although bumble bees and honey bees are capable of foraging great distances, well beyond 500 meters, most foraging activity in this example occurred close to natural woodlands. The level of foraging declined with greater distances from forest, and this suggests that woodlands are important source habitats for wild bees (Joshi et al. 2016). When this is applied to the Southeast Prairies, the realized area of pollination services by large social species, i.e. *Bombus* spp., may be

more contracted than the potential distribution modeled by the InVest software.

However, the Southeast Prairies is a large, well-connected landscape. The wide distribution of woodlands within it appears to have an important role, as a source of pollinator species, in the currently high level of ecosystem functioning compared to the landscape at its boarder.

The negative correlation of bee abundance and urban, suburban, or rural development seen in the current study is consistent with previous field experiments. Watson et al. (2011), for example, found a significantly negative association between development and wild bee species richness and abundance within 750 meters of studied apple orchards. Similarly, Bates et al. (2011) determined that the diversity and abundance of bees and hoverflies were significantly lower in areas with higher levels of urbanization. Importantly in the latter, however, response to habitat quality in terms of floral resource availability was positive in all contexts, but the composition of pollinator assemblages changed with the gradient of built land cover such that some species responded positively and others negatively. The large amount of impervious cover associated with urban and suburban landscapes can limit the density of ground-nesting bees, in particular (Jha and Kremen 2013b), but may also limit dispersal of even large, long-distance flyers such as bumble bees (Bhattacharya et al. 2003). Gene flow is especially limited in the latter by commercial, industrial, and transportation-related impervious surfaces (Jha and Kremen 2013a).

Persson and Smith (2013) determined that late-season declines in bumble bee abundances in simple landscapes are a consequence of resource-limited reproductive

capacity compared to complex landscapes in which bumble bee abundance increases throughout the season. This pattern may also manifest here since lower bee abundances are predicted in the greatly simplified landscape surrounding the Southeast Prairies. In the same study (Persson and Smith 2013), however, even regionally rare species were observed to persist, albeit at lower abundances, in simplified landscapes, possibly due to the inflow of queens from the neighboring complex landscape. Although a similar conclusion may hold for pockets of low predicted abundance within the boundaries of the Southeast Prairies BUL, in the surrounding landscape a threshold distance from the edge of the more complex, high abundance area likely exists, at which the presumed overflow supply would reach its limit and cease to sustain many species. Testing this hypothesis may be a fruitful endeavor for future research. Important considerations in such work, however, are results such as those of Williams et al. (2011), in which no examined landscape context provided sufficiently consistent resources for queen production in bumble bees.

Previous studies strongly suggest pollinator decline along gradients of agricultural intensification and habitat fragmentation (NRC 2006; Kremen et al. 2002; Ricketts et al. 2004; Larsen et al. 2005; Winfree et al. 2009). Some of these describe biased extinctions among certain bumble bees (Kleijn and Raemakers 2008) and specialists (Biesmeijer et al. 2006), with implications of subsequent decline in their functional roles, such as long-distance pollen dispersal, and this may ultimately reduce the resilience of pollination function (Larsen et al. 2005). Furthermore, Winfree et al. (2015) found that the pollination services of wild bees are primarily driven by the abundance of dominant

species. Bumble bees, as a dominant, albeit at-risk, group in this context may have a key role in pollination function across the Southeast Prairies landscape. Although the study area appears to be an oasis in its present condition, should encroaching agriculture along the border, or even within, the BUL increase, this landscape may cease to function as a sanctuary for these bees and their contribution to pollination. The distributions mapped in this study provide a foundation upon which conservation and restoration efforts may be based, by first identifying areas where implementation could be focused to maximize benefit.

Although biodiversity loss is broadly associated with diminished ecosystem functioning (Cardinale et al. 2012; Tilman et al. 2012), this association is not often tested in large ecosystems (Duffy 2009; Cardinale et al. 2012). Existing examinations of pollinator populations in landscapes suggest that whether potential resource-limited pollinator decline becomes realized depends on context-specific critical thresholds of resource availability required to maintain stable or increasing populations as well as the actual current availability (Dicks et al. 2015). Keitt (2009) simulated pollination services under various habitat conversion scenarios for several landscape contexts and found that the pollinator densities at the upper stable and the unstable tipping points at 50% habitat conversion provide only a very narrow tolerance for disturbance before species are pushed to local extinction. Here, indices of foraging bee abundances decline more sharply when land area with crop cover passes 16.7%, and do not continue to increase as the proportion of suitable forage cover passes 68.3% (Fig. 5.18). These results may initially appear encouraging in consideration of recent studies by Dicks et al. (2015),

Carvell et al. (2014) and Redhead et al. (2016), for which surprisingly little flower-rich habitat was sufficient to meet the pollen demands of bumble bees and *Andrena* spp., with lower estimates of 2% and 1-3% of each 100 hectares of farmland, respectively, in enhanced agri-environment schemes in Europe. Importantly, however, the authors recognize that the high-end estimates of resources required to meet pollen demands of wild bees, which are met when 44% of the farmed landscape remains unconverted, are beyond the reach of any current packages of agri-environment schemes (Dicks et al. 2015). This estimate is only slightly greater than the lower threshold of forage cover (37%, Fig. 5.18b) identified in this study. Kremen et al. (2004) report a similar range of natural area requirements for sufficient pollination of watermelon by native bees, with 40% or more within a 2.4 km radius of farms. Pollination was still sufficient at a lower percentage, 30% or more, at half the distance from farms (Kremen et al. 2004).

Another important consideration when comparing these results to Dicks et al. (2015) is the subset of wild bees examined, particularly the bumble bees. These are large, long-distance foragers and therefore, the minimal requirements estimated at 2% are not representative of area thresholds of suitable forage needed to sustain populations of small species, which were considered here. Subsequent studies have acknowledged that such pollinator-focused management schemes provide resources to a limited suite of bee species, and further, that most solitary species utilize forage in the wider environment rather than that in provisioned plots (Wood et al. 2017).

It's understood that foraging distances are flexible, depending on resource distribution (Carvell et al. 2012). Although long-distance foragers such as bumble bees

can easily adjust foraging effort to access resources distributed within 100-hectare blocks of farmland as examined by Dicks et al. (2015), the costs of long-distance foraging may be unsustainable for smaller species. It's important to consider such limitations when examining threshold areas, as was done here. Thresholds in this study were calculated from InVEST service indices which consider the resource needs of the combined assemblage of functional guilds in order to provide a coarse-grain estimate of the status of general pollination function that can be used to inform broad pollinator conservation strategies. Therefore, these do not depict differences in thresholds for the various suites of bee species within the assemblage. However, because thresholds likely vary between species, especially between the largest and smallest species, Robbins (2009) suggests converting habitat availability thresholds into probabilities of persistence or extinction so that comparisons can be made between species using equivalent units. Future work could design these conversions for different suites of wild bee species and build upon the findings of this work by examining whether pollination function follows the response of different functional guilds to changes in landscape composition. These tools could also be implemented at larger scales, such as entire states and regions, to identify other areas of concern and potential hotspots of bee diversity in the Great Plains and other ecosystems.

Conclusion

By calibrating the InVEST pollination models to reflect the capacities of different suites of species to reach suitable forage, as well as the differences in the availability of suitable forage that arise from the distribution of different kinds of nesting habitat,

valuable insight was attained regarding the common mechanisms underlying the distribution patterns of foraging bees. More specifically, this study demonstrates how the abundance of foraging bees expected to utilize marginal habitat, such as that provided along roadsides, in developed areas, or in crop field margins, changes with the extent of habitat conversion in the wider landscape. Perhaps the greatest contribution of this study is the estimation of thresholds for important land cover types, particularly cropland and suitable forage, which address the challenging question of “how much habitat is enough to maintain ecosystem functioning?” Within the area designated BUL, this aspect of functioning appears to remain highly operative, but the limits of this functioning beyond the BUL, and even throughout the state or region, warrant further investigation. Importantly, by estimating extinction risks for different suites of species, future studies could identify the most vulnerable of wild bees to changes in land use around these thresholds. Furthermore, the InVEST software would be a useful tool for additional work and has the benefit of other models for quantifying ecosystem functioning in addition to pollination. By employing these other models, an assessment of this grassland ecosystem’s status of multifunctionality, and how this corresponds to biodiversity beyond pollinators, could be performed.

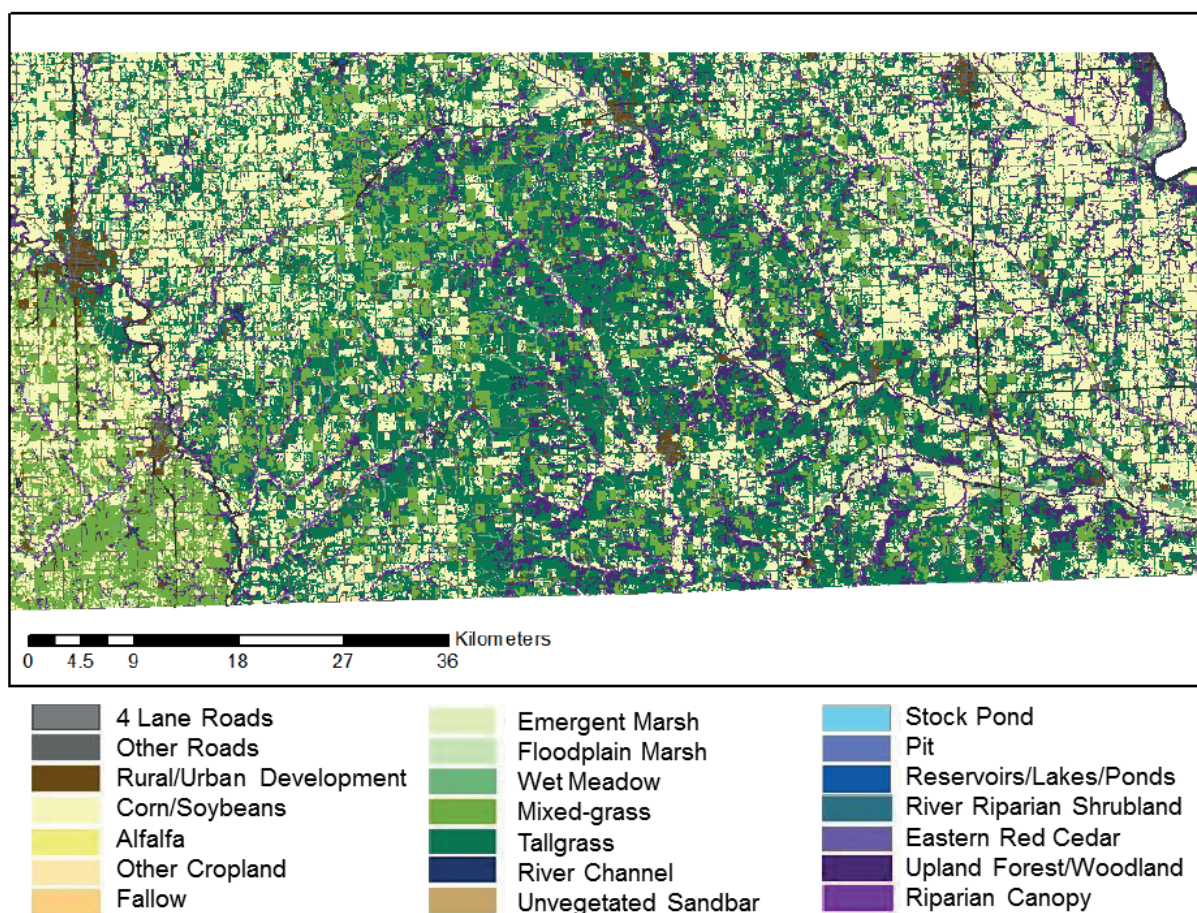


Figure 5.1. Land cover types of the Southeast Prairies Biologically Unique Landscape. The map shows the distribution of land cover across the study area using simplified land use and land cover classifications. Paved roads and highways are included in 4 Lane Roads and gravel and dirt roads are combined in Other Roads. Corn and soybeans are the dominant agricultural land uses, alfalfa is isolated because of its potential to provide forage for wild bees, and sorghum and wheat comprise remaining known cropland cover types. CRP and grazed pasture grasslands were included within the mixed-grass classification rather than tallgrass prairie. Waterways and water bodies, sandbars and pits were considered resourceless for wild bees. Classifications are based on data with 30-meter resolution.

Table 5.1. Classification of wild bees into guilds by body size, sociality, nesting strategy, and estimated foraging capacity. Classification criteria are listed for each trait used to model bee abundances according to resource distribution in the InVEST pollination model.

Final guild assignment	Genera (no. of species)	Maximum body size	Social classification	Nesting strategy	Foraging capacity (m)
Large social	<i>Bombus</i> (7)	13-25mm	Social	Cavity	3016
Small social	<i>Halictus</i> (2)	8-13mm	Social	Ground	600
Large ground	<i>Anthophora</i> (6) <i>Melissodes</i> (7) <i>Svastra</i> (1) <i>Xenoglossa</i> (1)	12-16mm	Solitary	Ground	584
Small ground	<i>Agapostemon</i> (3) <i>Augochlorella</i> (1) <i>Augochloropsis</i> (1) <i>Calliopsis</i> (1) <i>Lasioglossum</i> (3) <i>Melissodes</i> (2) <i>Protandrena</i> (1)	5-11mm	Solitary	Ground	333
Large wood	<i>Xylocopa</i> (1)	18-23mm	Solitary	Wood	2813
Medium wood	<i>Megachile</i> (3)	9-17mm	Solitary	Wood	657
Small wood	<i>Anthidiellum</i> (1) <i>Augochlora</i> (1) <i>Ceratina</i> (1) <i>Dianthidium</i> (1) <i>Hoplitis</i> (1) <i>Osmia</i> (1)	5-9mm	Solitary	Wood, twigs, or under bark	160

Notes: The number of species considered within each genus is given in parentheses. Maximum body size indicates the range of maximum body sizes for the species included within each genus. Only eusocial species with a queen as the sole egg-laying female were classified as social and gregarious species were considered solitary. Nesting strategy indicates each guild's nesting behavior or the substrate in which nest-building occurs. Foraging capacities are mean distances determined from published experiments on species within these genera in which body size was explicitly considered (studies are summarized by Zurbuchen et al. 2010b) and fit within the ranges based on body size predicted by Greenleaf et al. 2007.

Table 5.2. Habitat suitability scores for land cover and land use classes within and surrounding the Southeast Prairies Biologically Unique Landscape. A score (0-1) is given for each land cover class to depict the potential to provide nesting and forage resources for wild bees. Nesting suitability was estimated for cavity-, ground-, and wood- or twig-nesting guilds.

General land category	Land cover and land use classification	Nesting suitability			Forage suitability
		Cavity	Ground	Wood/twig	
Grasslands	Mixed grass prairie	0.58	0.81	0.15	1.00
	Tallgrass prairie	0.58	0.81	0.15	1.00
	Wet meadow	0.15	0.16	0.29	0.88
Woodlands	Upland forest	0.72	0.51	0.97	0.53
	Eastern red cedar	0.51	0.44	0.89	0.42
	Riparian canopy	0.67	0.09	0.84	0.48
	River riparian shrubland	0.68	0.76	0.89	0.56
Croplands	Corn	0.09	0.14	0.14	0.09
	Soybeans	0.13	0.22	0.14	0.23
	Sorghum, wheat, other	0.14	0.15	0.11	0.11
	Alfalfa	0.13	0.22	0.14	0.31
	Fallow	0.23	0.40	0.21	0.32
Development	Rural	0.21	0.33	0.20	0.23
	Urban/Suburban	0.14	0.08	0.12	0.17
Roads	Paved 4- or 2-lane highways	0.19	0.28	0.15	0.43
	Gravel, dirt, other local	0.25	0.33	0.16	0.41
Other	Uncultivated floodplain	0.25	0.20	0.34	0.48
	Badlands or other uncultivable, minimal vegetation	0.08	0.82	0.05	0.33
	Emergent marsh	0.25	0.14	0.34	0.48
Resourceless	Lakes, lagoon, pit, ponds, reservoirs, stock ponds, river channel, unvegetated sandbar	0.00	0.00	0.00	0.00
		0.00	0.00	0.00	0.00

Notes: Nesting and forage suitability scores are either those used for the pollination model of ESTIMAP (Zulian et al. 2013), which has been used for mapping services of wild bees across Europe, or scores derived via expert opinion used by Koh et al. (2016) to evaluate the status of pollination services across the United States. When multiple potential suitability scores were available, selection of the most appropriate score was based on land cover quality within a tallgrass prairie-specific context as assessed by Hines and Hendrix (2005).

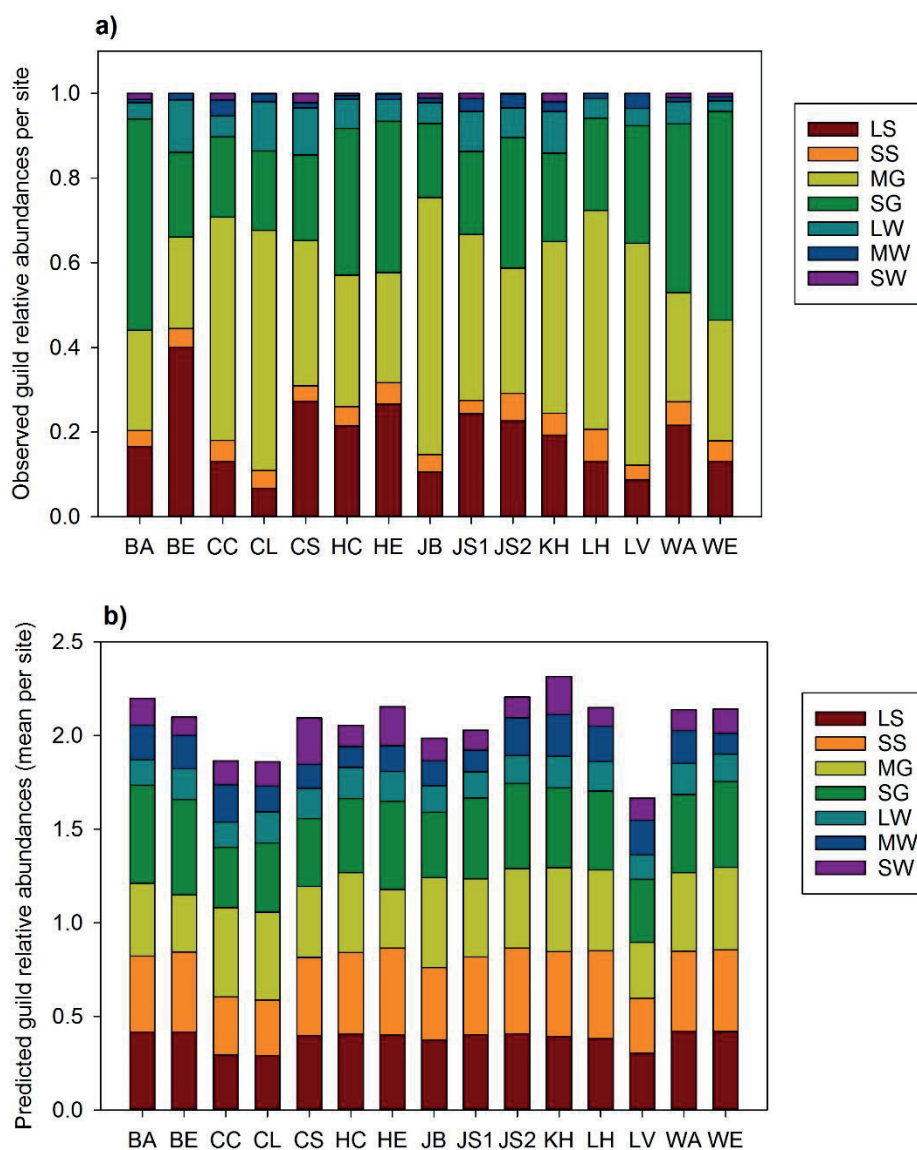


Figure 5.2 Observed and predicted relative abundances of bees within each of seven functional guilds in the Southeast Prairies Biologically Unique Landscape. The mean relative abundances are shown for each of 15 study sites where a) wild bees were collected, and b) visiting bee abundances were predicted using the InVEST pollination model. Guilds include large social species (LS), small social species (SS), medium-large ground-nesters (MG), small ground-nesters (SG), large wood-nesters (LW), medium wood-nesters (MW), and small wood-nesters (SW). Observed relative abundances are the proportion of individuals within each guild collected from each site. The predicted relative abundances are the mean abundance indices given by the InVEST pollination model for each guild and study site.

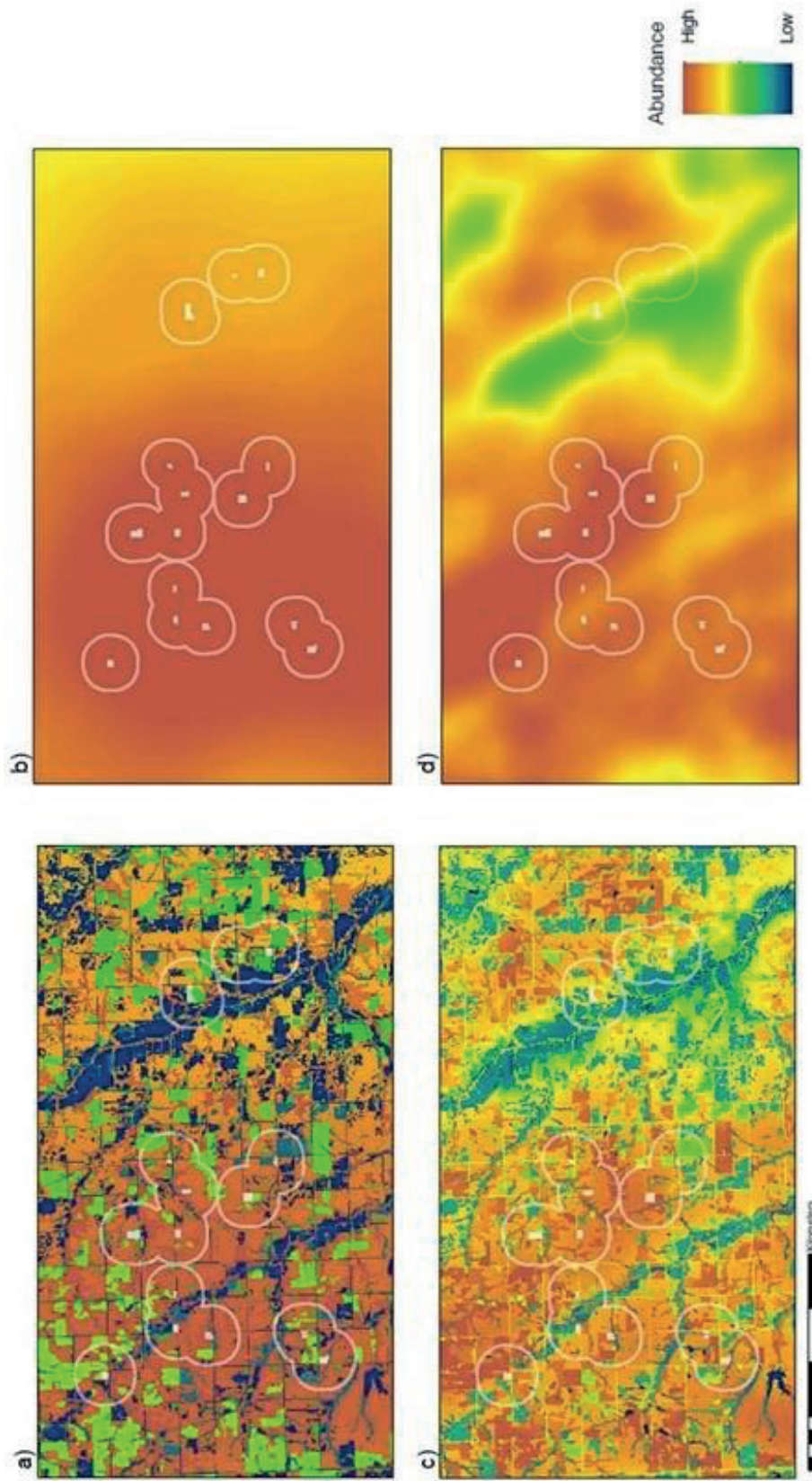


Figure 5.3 Modeled distribution of nesting and foraging social bees among 15 study sites within the Southeast Prairies BUL and the surrounding landscape within 1200 meters of each site. Estimates of nesting and foraging bee abundance are mapped for each cell in the landscape (30 x 30 m resolution per pixel) for large, social cavity-nesters with large foraging capacities (a, b) and small social ground-nesters with moderate foraging distances (c, d). Areas of high predicted abundance are shown with hot colors (reds, oranges, and yellows). Areas of low predicted abundance are shown with cool colors (greens and blues)

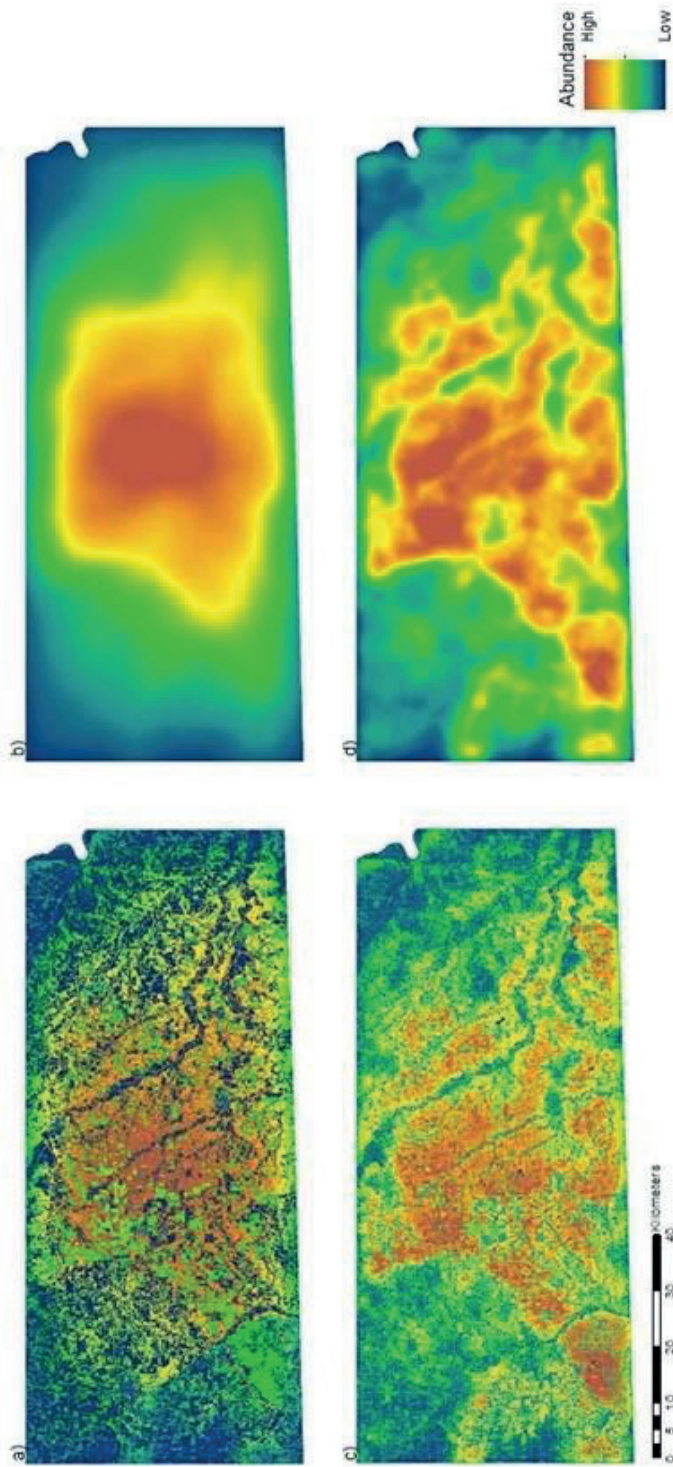


Figure 5.4. Modeled distribution of nesting and foraging social bees across the Southeast Prairies Biologically Unique Landscape. Estimates of nesting bee abundance for large social bumble bees (a) and small social sweat bees (c) are mapped, along with estimated visitation rates (b, d) to each cell in the landscape. Areas of high predicted abundance are shown with hot colors (reds, oranges, and yellows). Areas of low predicted abundance are shown with cool colors (greens and blues).

Table 5.3. Abundance indices for nesting and foraging bees estimated with the InVEST pollination model for seven guilds of wild bees across the Southeast Prairies BUL. The minimum, maximum, and mean predicted relative abundance indices are listed for large (LS) and small (SS) social bees; medium to large solitary ground-nesting bees (MG); small solitary ground-nesting bees (SG); and large (LW), medium (MW), and small (SW) solitary wood-nesting bees. Standard deviation is given in parentheses.

InVEST index	Large social species (LS)	Small social species (SS)	Medium ground- nesters (MG)	Small ground- nesters (SG)	Large wood- nesters (LW)	Medium wood- nesters (MW)	Small wood- nesters (SW)
Nesting							
Mean (SD)	0.198 (0.197)	0.250 (0.164)	0.253 (0.168)	0.262 (0.183)	0.087 (0.145)	0.095 (0.155)	0.099 (0.156)
Min	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Max	0.678	0.663	0.687	0.735	0.681	0.813	0.888
Foraging							
Mean (SD)	0.184 (0.101)	0.246 (0.110)	0.250 (0.114)	0.260 (0.130)	0.081 (0.039)	0.094 (0.051)	0.100 (0.075)
Min	0.012	0.019	0.018	0.011	0.004	0.003	0.000
Max	0.423	0.514	0.555	0.662	0.170	0.294	0.427

Bee abundance indices are used as proxies of the pollination services delivered by foraging bees and are modeled for the landscape using InVEST software (Lonsdorf et al. 2009) developed within the Natural Capital Project ©. The means given above are averaged across the entire Southeast Prairies BUL.

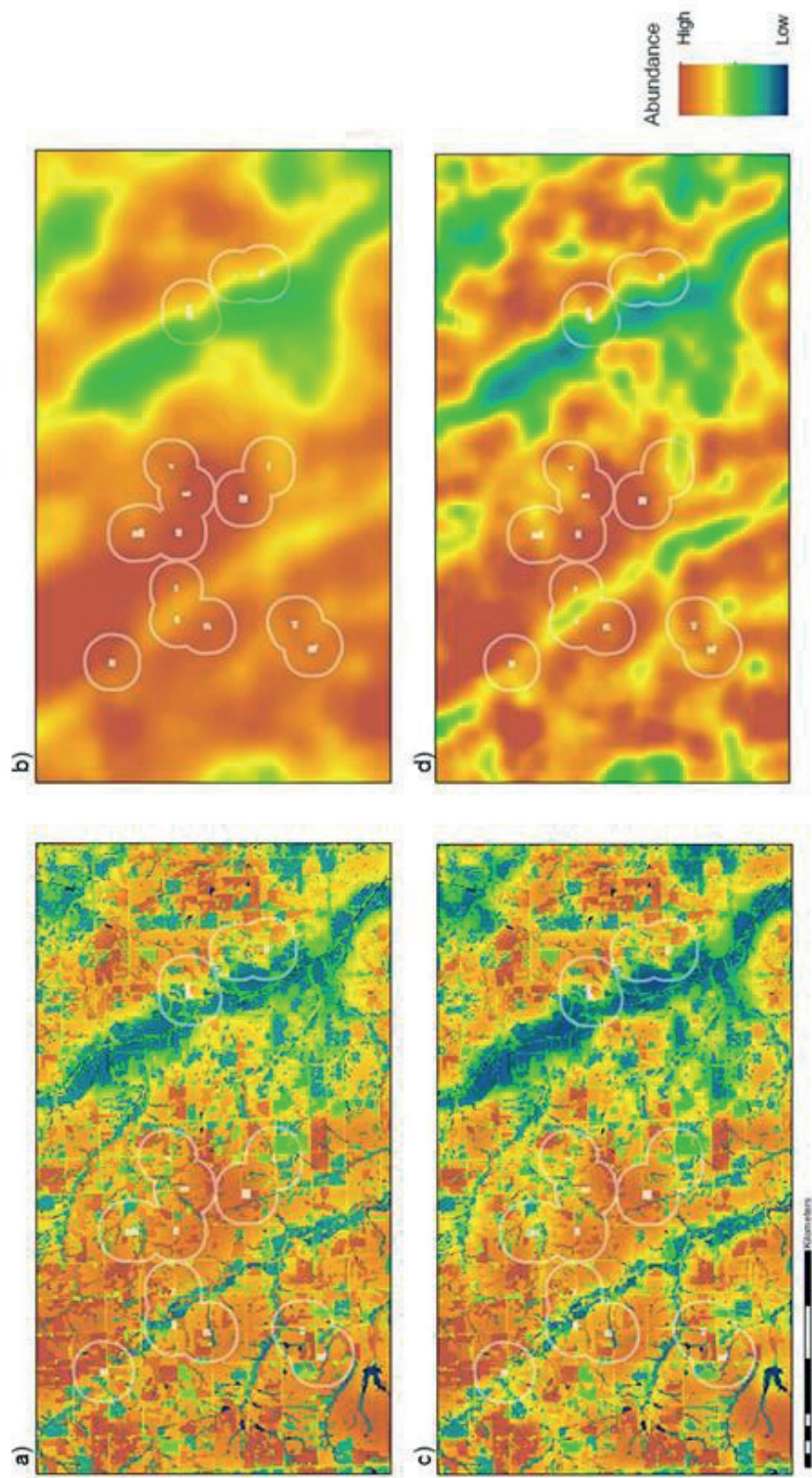


Figure 5.5. Modeled distribution of nesting and foraging solitary ground-nesting bees among the 15 study sites and surrounding landscape within 1200m of each site within the Southeast Prairies Biologically Unique Landscape. Estimates of nesting and foraging bee abundance are mapped for each cell in the landscape for large (a, b) and small solitary ground-nesters with moderate foraging distances (c, d). Areas of high predicted abundance are shown with hot colors (reds, oranges, and yellows). Areas of low predicted abundance are shown with cool colors (greens and blues).

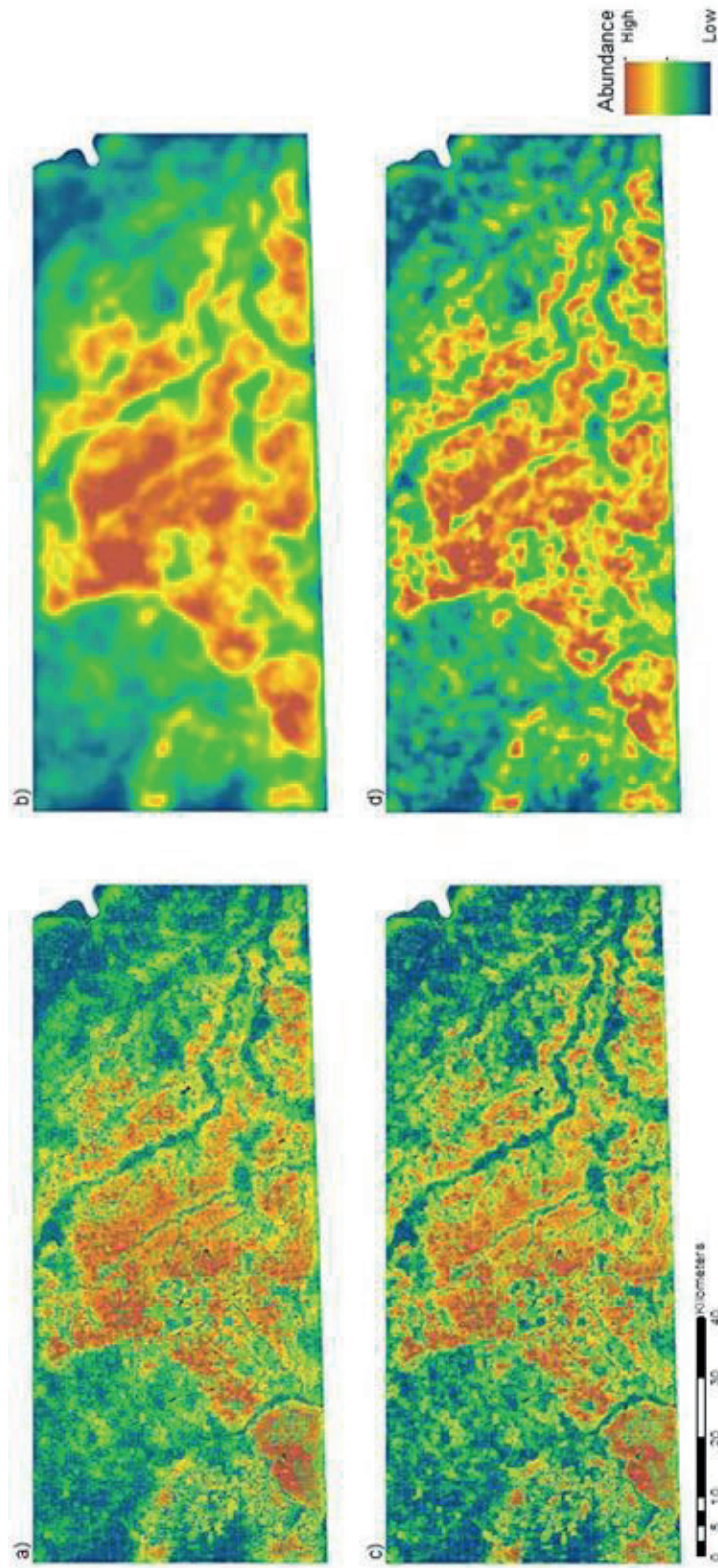
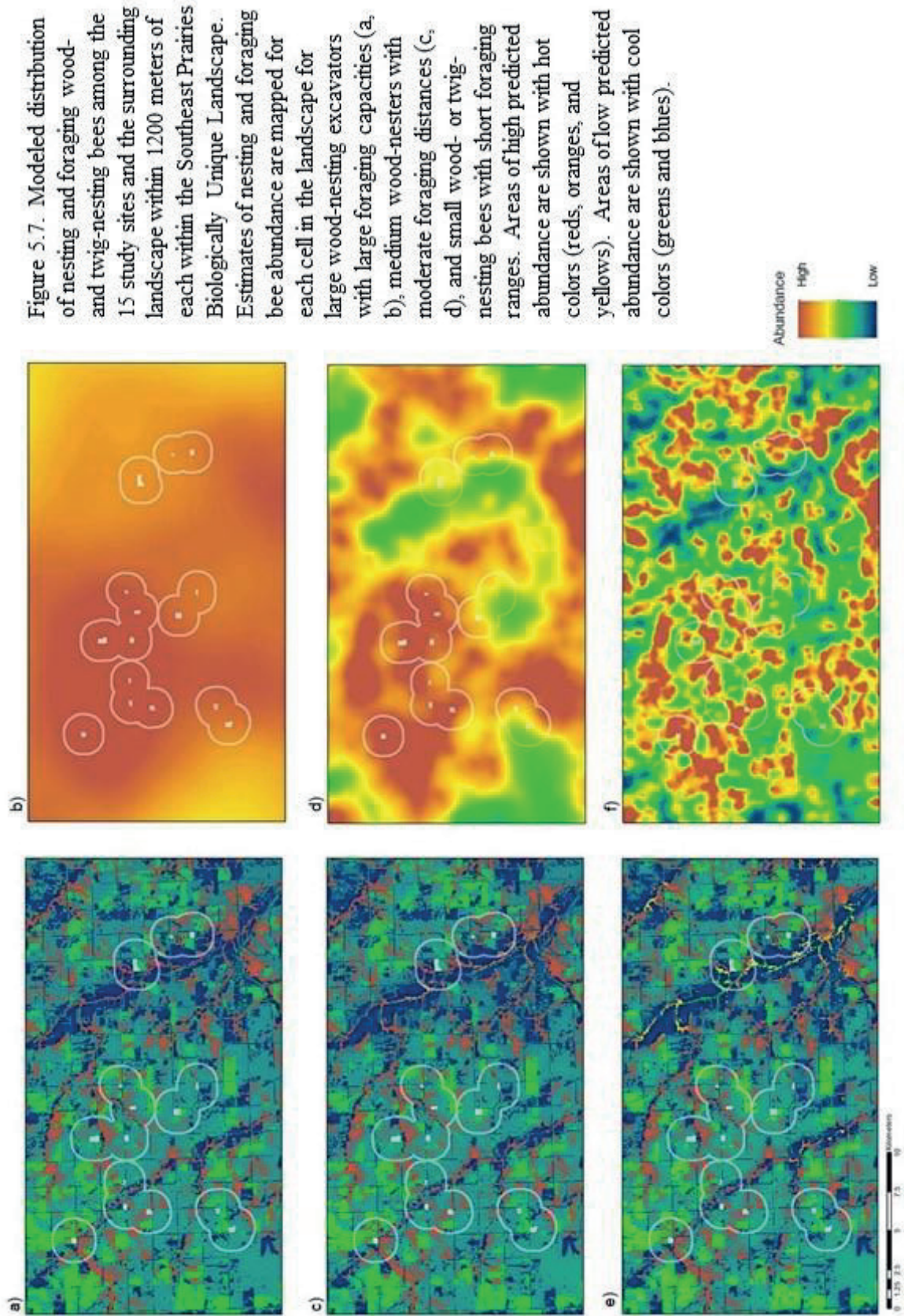


Figure 5.6. Modeled distribution of nesting and foraging ground-nesting bees across the Southeast Prairies Biologically Unique Landscape. Estimates of nesting and foraging bee abundance are mapped for each cell in the landscape for large ground-nesters with greater foraging capacities (a, b) and small ground-nesters with shorter foraging distances (c, d). Areas of high predicted abundance are shown with hot colors (reds, oranges, and yellows). Areas of low predicted abundance are shown with cool colors (greens and blues).



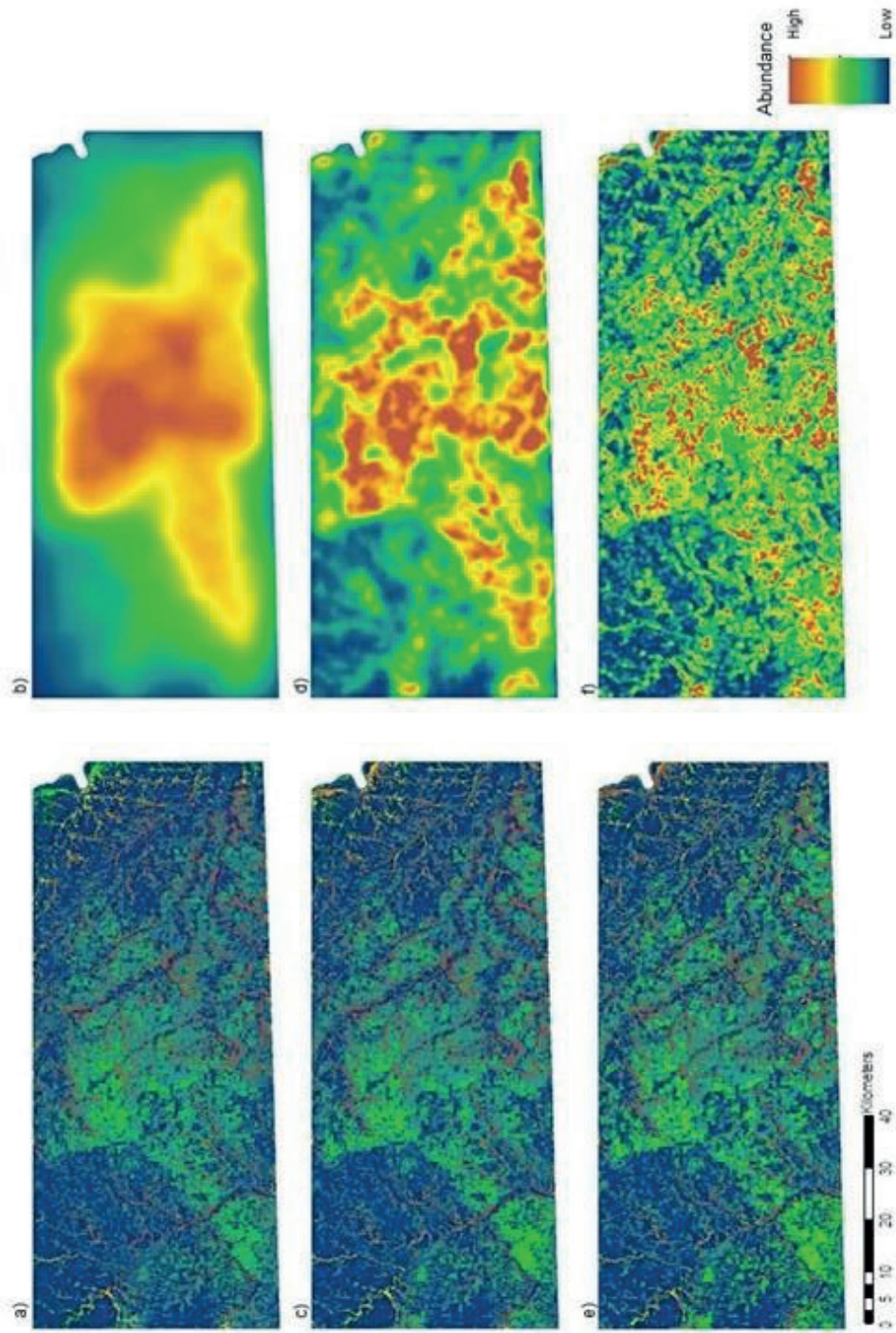


Figure 5.8. Modeled distribution of nesting and foraging wood- and twig-nesting bees across the Southeast Prairies BUL. Estimates of bee abundance are mapped for each cell in the landscape for large (a, b), medium (c, d), and small wood-nesting bees. High estimates are shown with hot colors (reds, oranges, and yellows). Areas of low predicted abundance are shown with cool colors (greens and blues)

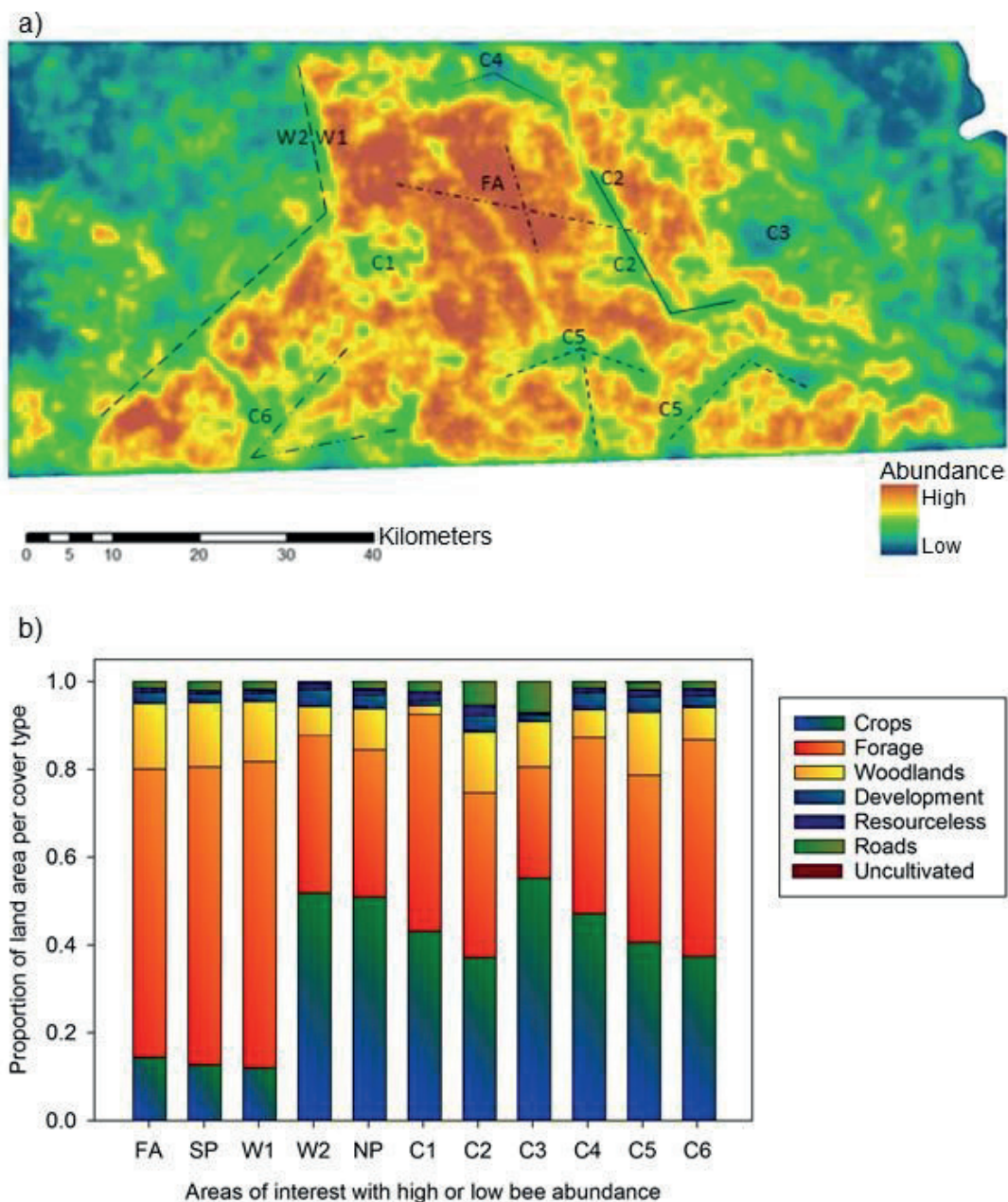


Figure 5.9. Comparison of land cover types within areas of high and low wild bee abundances in the Southeast Prairies Biologically Unique Landscape. The average relative abundances of combined social and solitary guilds are depicted with areas of interest a) identified and b) plotted by the composition of land cover types. Areas of interest include the focal study area (FA), combined area of high (yellow-red) relative bee abundances (SP), the western edge of the BUL (W1 and W2), combined area of low (green-blue) relative bee abundances (NP), and six pockets of low average foraging index within the BUL (C1-C6).

Table 5.4. Results of correlations of relative bee abundances and the proportion of land area covered by seven broad classes of land cover types in the Southeast Prairies and surrounding landscape. The correlation coefficient, p-value, and number of samples are listed for the total modeled area of the Southeast Prairies (overall), the areas within the Southeast Prairies with high relative bee abundances (SP) and areas of low relative bee abundance (NP). These values are also given for the mean relative bee abundances within each cover type.

Location	Crops	Forage	Woodlands	Roads	Development	Uncultivated	Resourceless
Overall (SP & NP)							
Total area	-0.718 <0.001	0.700 <0.001	0.048 0.723	0.286 0.086	-0.301 0.036	-0.057 0.818	-0.250 0.063
Per cover type	-0.503 <0.001	0.736 <0.001	0.174 0.200	0.509 0.001	-0.271 0.060	0.106 0.668	-0.164 0.226
No. samples	57	57	56	37	49	18	56
High abundance (SP)							
Total SP area	0.039 0.854	0.212 0.310	0.101 0.629	0.260 0.307	0.335 0.148	-0.174 0.826	0.440 0.059
Per cover type	0.215 0.303	0.086 0.683	0.132 0.530	0.287 0.258	-0.044 0.851	-0.246 0.754	0.292 0.163
No. samples	25	25	25	17	20	4	24
Low abundance (NP)							
Total NP area	-0.345 0.043	0.577 0.001	0.397 0.027	0.411 0.071	-0.245 0.197	0.042 0.880	-0.356 0.056
Per cover type	-0.392 0.026	0.612 <0.001	0.268 0.144	0.586 0.007	-0.198 0.300	0.310 0.271	-0.260 0.149
No. samples	32	32	31	20	29	14	32

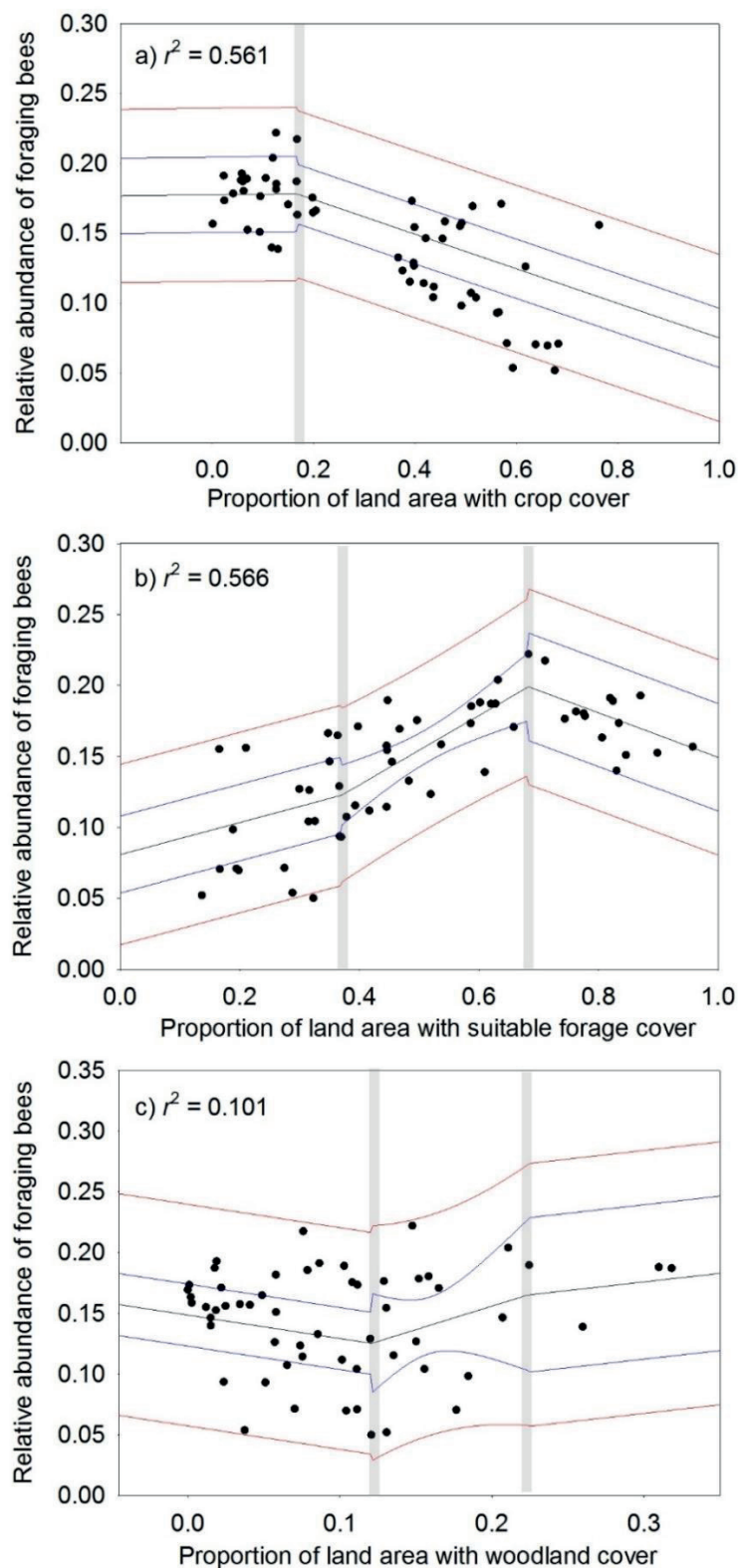
Notes: Pearson product moment correlations were used where data passed Shapiro-Wilk normality tests and are shown in black. Spearman rank correlations were used otherwise and are shown in blue. Significant correlations are shown with boldface type. Significance was set at 0.007 with Bonferroni corrections for multiple comparisons

Table 5.5. Results of multiple response permutation procedures to compare bee abundances between areas of high and low abundance in the Southeast Prairies (SP) and surrounding landscape (NP). The mean (\pm 1 s.e.) relative abundances of foraging bees for each of the five correlated land cover types are listed. The average Sørensen distances, test statistics (T), chance-corrected within-group agreement (A), and p -values for each MRPP are given.

Mean or MRPP	Forage	Crops	Woodlands	Roads	Development
Means (s.e.)					
SP	0.402 (0.018)	0.171 (0.016)	0.295 (0.023)	0.166 (0.020)	0.199 (0.014)
NP	0.426 (0.015)	0.258 (0.019)	0.198 (0.014)	0.112 (0.011)	0.112 (0.014)
No. samples					
SP	25	25	25	15	20
NP	32	32	32	19	29
MRPP					
SP distance	0.1316	0.2851	0.2487	0.3429	0.2511
NP distance	0.1113	0.1713	0.2525	0.3488	0.2768
T statistic	-0.2795	-8.0742	-6.5462	-12.968	0.9049
A	0.0035	0.0968	0.0818	0.2648	-0.0125
p -value	0.2780	0.0001	0.0005	< 0.0001	0.9130

Notes: Relative abundances are predicted indices of foraging bees per patch of land cover resulting from the InVEST pollination model (Lonsdorf et al. 2009). The p -values represent the probability of obtaining an equal or smaller delta from the MRPP.

Figure 5.10. Results of two- and three-segmented piecewise regressions to identify thresholds of land area of the three relevant cover types for foraging bees. Regressions are shown with breakpoints indicating the threshold proportions of land area covered by a) crops, b) suitable forage, and c) woodlands at which point the relative abundances of foraging bees change. Models converged in 18, 21, and 12 iterations, respectively, and tolerance was satisfied for each scenario. Adjusted R^2 values are given within each plot. The 95% confidence intervals are indicated with blue and the 95% prediction intervals are indicated with red. The breakpoints and transition areas which represent the threshold values are grey.



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CONCLUSIONS

Levin (1999) described the nature of ecosystems as complex and adaptive, stating that “nature is not fragile, [but] what is fragile are the ecosystems on which humans depend.” Elmqvist and colleagues (2003) highlighted the essential role of diversity, particularly within functional groups, in creating the adaptive capacity of ecosystems. The body of research which supports that greater diversity in ecosystems providing greater anthropogenic benefits has grown substantially (Green et al. 2005; Butchart et al. 2010; TEEB 2010), and this has been used to justify biodiversity conservation on the grounds of maintaining these ecosystem services. Yet the definition of “service” to describe pollination, as direct economic benefit to humans, is one argument I’ve tried largely to avoid throughout this dissertation. In that context, biodiversity conservation is a means of maintaining or enhancing crop pollination services. Although crop pollination is an ecosystem service that arises from the broader ecological function of pollination, and wild bees do often significantly contribute to productivity for many crops (Free 1993; Gallai et al. 2009), not only are there few pollinator-dependent crops in the study area, but recent work (i.e. Kleijn et al. 2015) reveals that arguments for the conservation of biodiversity for crop pollination do not sufficiently justify the protection of many threatened species because those which provide the greatest delivery of crop pollination services comprise only a small subset of known species. Instead, because of the consensus that biodiversity is declining at an unprecedented rate on a global scale, that this threatens the persistence of species and ecosystems (Butchart et al. 2010; TEEB 2010), and that among the greatest challenges for conservation planning is estimating how much ecosystem is enough to maintain functioning (Blann 2006), it was important to

keep the concept of “service” in the broader context of ecosystem functioning since pollination represents only one component of a functional grassland. Therefore, this project describes the diversity of wild bee assemblages, how patterns of resource utilization differ between types of grasslands, the local- and landscape-level drivers of abundance and diversity, the current status of pollination function in an agricultural landscape, and the thresholds of land conversion that are important to this component of ecosystem functioning in a tallgrass prairie grassland.

I began by addressing certain knowledge gaps recognized by the Nebraska Natural Legacy Project with the characterization of wild bee species assemblages from three Biologically Unique Landscapes. Ordination analyses revealed three distinct communities, with the greatest similarity between the Southeast Prairies and Platte Prairies, and least similarity between the Southeast Prairies and Holt CRP communities. Diversity estimates were greatest for the Southeast Prairies and each of the three communities exhibited high dominance, particularly by *Melissodes*. The Southeast Prairies were additionally dominated by *Bombus* and *Agapostemon*, the Holt CRP site by *Eucera* and *Agapostemon*, and the Platte Prairies by *Diadasia*. There was significant species turnover within each study location over the course of the season but few differences between the habitat or planting types within them were observed. The abundance of bumble bees in the Southeast Prairies may be especially useful in future conservation planning. *B. pensylvanicus*, in particular, is listed as “vulnerable” on the IUCN Red List of Threatened Species because of major declines in range, persistence, and relative abundance (Hatfield et al. 2015). Its dominance in the Southeast Prairies may be indicative of sufficient high-quality habitat to sustain a reservoir of this and other

pollinator species. This may provide evidence that supports continued efforts to maintain the connectivity and quality of this landscape for conservation of wildlife and ecosystem services.

When the species assemblages of the Southeast Prairies were further categorized by functional traits, few differences again were identified between the remnant prairie, grazed pasture, and CRP grassland habitats from which bees were collected. Instead, the functional composition of wild bees appears to be largely driven by floral resource availability, rather than grassland type. Functional richness of wild bees increases with forb diversity, as do the number of pollen-bearing bees and the number of pollen types identified from pollen-bearing bees. Furthermore, matches often occurred for blooming forbs and pollen types in indicator species analyses, although forb species richness was significantly greater in remnant prairie sites than either grazed pasture or CRP. A significantly greater number of pollen-bearing bees were also collected in remnant prairie, possibly indicating a concentration of foraging activity within haymeadows. In all grassland types, social, long-distance foragers (i.e. *Bombus* spp.) bore pollen more frequently than other functional guilds. Therefore, bumble bees appear to be an important group of pollinators in the Southeast Prairies. The trait-based approach used here, which incorporated pollen analysis as a proxy of resource utilization, helped identify which guilds and in which habitat types bees carry out the bulk of pollination. Future work may build upon this by identifying whether functional compensation or replacement occurs in contexts where whole suites of species have declined.

The blue vane traps used in this research easily trigger a dilemma of conscience given the benefits and consequences of their employment. They are highly efficient and

bypass many issues of conventional pan traps for sampling wild bees, such as handling wet specimens and the logistics of hauling traps and fluids across large sites or landscapes. In this study, the blue vane traps allowed for pollen analysis from the bodies of bees because they were not captured in a liquid that would rinse them. However, too many were taken from these ecosystems. Although bees are typically still alive upon collection, and there is potential for catch and release sampling, this depends on the ability of the sampler to accurately identify active bees. The microscopic nature of the identifying characteristics of many species presents obvious complications. That said, and considering the quantity extracted in this study, the bees that such research aims to better understand and protect would be well-served by this practice. Particularly problematic is that their use in the spring and early summer, when bumble bee queens are working to establish their nests, may well extinguish whole colonies. This could interrupt an entire local population since only mated queens are able to propagate a functioning class of workers, which in turn sustain her until the colony is able to produce the reproductive class. The loss of a queen ends the life cycle that would continue the species into the next year. Although useful for gathering baseline data on wild bee populations, monitoring efforts should continue with alternatives to blue vane traps that collect fewer individuals, or by identifying and releasing live, healthy bees.

Results of multi-model inference reiterated the importance of floral resource availability for supporting a robust community of wild bees. However, bee responses were influenced by a combination of local and landscape factors, and the scale at which bees responded to landscape factors largely corresponded to foraging capacity. The inclusion of multiple connectivity metrics in this analysis, and graph-theoretic metrics in

particular, helped to identify the network components of mosaic landscapes that are important to different suites of species based on landscape composition, habitat quality, and species' resource requirements.

Forb abundance was an important predictor of ground- and wood-nesting bee abundance, along with intra-patch connectivity and the amount of crop cover surrounding a forage patch for the former. The dispersal potential to or from the forage patch and the amount of adjacent wetland cover were also important for the latter. In contrast, woodlands and the amount of road cover surrounding a forage patch were the best predictors of cavity-nesting bee abundance, while blooming forb species richness and connectivity were of secondary importance. Local factors were secondary to connectivity, woodlands and wetlands surrounding a forage patch for eusocial bees collectively as well, while, in addition to the generalized betweenness centrality of the forage patch, forb richness and the amount of woodland cover within the patch were better predictors of solitary bee abundance than other landscape factors. In broad context, these results are in agreement with previous work which demonstrates that heterogeneity in the landscape is important for preserving biodiversity in agricultural landscapes (Tscharntke et al. 2005), especially for the conservation of wild bees (Kremen et al. 2007). It's also been observed that many species can persist in agricultural landscapes where low intensity management is practiced (Mayfield and Daily 2005; Tscharntke et al. 2005) due, in part, to complementary habitat use which follows spatiotemporal patterns in floral resource availability (Mandelik et al. 2012). Considering this, conservation efforts can take a broader, cross-habitat perspective for persistence of pollinator populations and the maintenance of pollination function

(Mandelik et al. 2012). Such an approach would better encompass the resource requirements of multiple suites of wild bees.

The InVEST pollination models that were used in the final chapter extend these relationships of bee abundance to resource availability to the entire Southeast Prairies BUL and the surrounding area. By calibrating the models to reflect habitat availability based on the distribution of different land cover types, and assigning suitability scores to all cover types, I was able to identify areas where bee abundances are expected to be consistently high or low among the different suites of species. This allowed for an examination of the common mechanisms underlying the predicted distribution patterns of foraging bees from which thresholds of habitat conversion and suitable habitat availability were estimated. The importance of marginal habitat along roadsides, in crop field margins, and within developed areas may increase as the extent of habitat conversion changes from areas of high to low predicted foraging bee abundances. Perhaps the greatest contribution of this study, however, is the estimation of thresholds for important land cover types which address the challenging question of “how much habitat is enough to maintain ecosystem functioning?” Although no minimal requirement of woodland cover was detected here, the minimal area of suitable forage cover was near 37%, which approaches the upper range of the minimal threshold of floral requirements that meet the pollen needs of bumble bees (Dicks et al. 2015) and is within the minimal range of natural habitat for sustaining other wild bees in farmland (Kremen et al. 2004). In contrast, the maximum tolerance of cropland cover was near 17%, beyond which foraging bee abundances declined. Considering that previous work identified only a narrow range where further disturbance can be tolerated before bee species experience

local extinction at higher levels of habitat conversion (Keitt 2009), designing appropriate conversions of habitat availability thresholds to persistence or extinction probabilities (Robbins 2009) is a key next step to assess species' vulnerabilities and to design conservation strategies that address the needs of a broad range of threatened species.

It's important, as Blann (2006) describes, for conservation strategies to take into account species' habitat needs within the context of their native landscape's history. With this approach, what is 'adequate' or 'enough' depends on the influence of the matrix, the connectivity of suitable habitat patches, and the quality of those patches. That this project examined each of these perspectives and is a valuable contribution to the collective understanding of how wild bee communities are structured in this prairie landscape. It describes the influence of habitat quality, resource availability and landscape components on the bee community from the perspectives of traits, functional guilds, species, and assemblages, which was important for better understanding of the role of wild bees in pollination functioning within this grassland ecosystem. Future work may expand upon this information and use it to design broad-reaching, multi-scale, cross-habitat conservation strategies which encompass the diverse resource requirements of multiple suites of wild bees. Such a comprehensive approach ensures the persistence of wild bee communities and the maintenance of the pollination services they provide. This in turn supports resilience grasslands since the persistence of their biodiversity depends on maintain and restoring ecological connections between species.

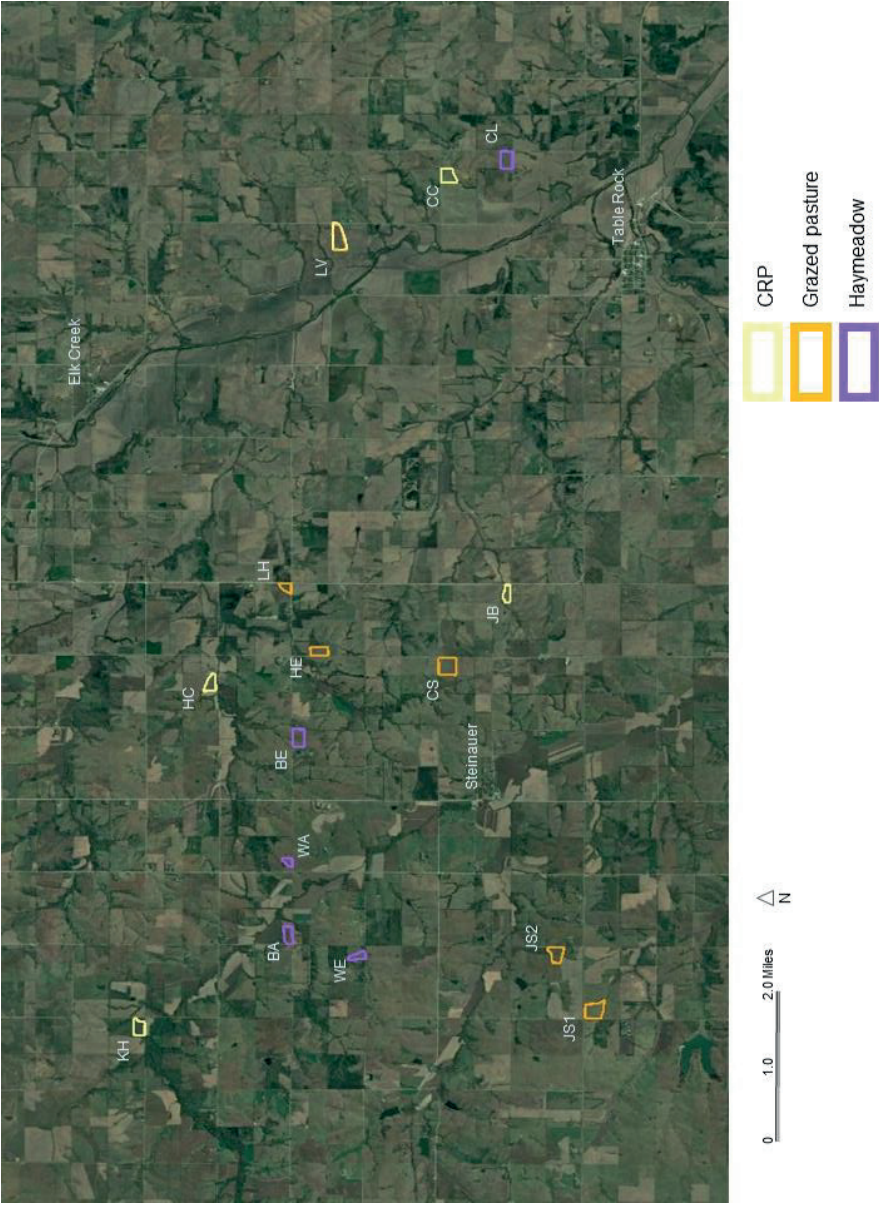
This study is merely a snapshot in time, and it has occurred as the Southeast Prairies is on the verge of a generational shift in land ownership. Therefore, stewardship of this unique landscape will be subject to any accompanying philosophical differences in

how land can or should be used, or perhaps more importantly, how one's life is lived in relation to that land. This small hotspot may stand resilient, be swallowed by the ever-encroaching croplands, or transition to something in between. In any scenario, the network of human choices that bring about the fruition of the future are as dynamic as the ecology underpinning the species associations in this dissertation. Levin may be right in that nature is not fragile, but human actions matter. As one of the interacting species of all ecosystems, we leave our mark.

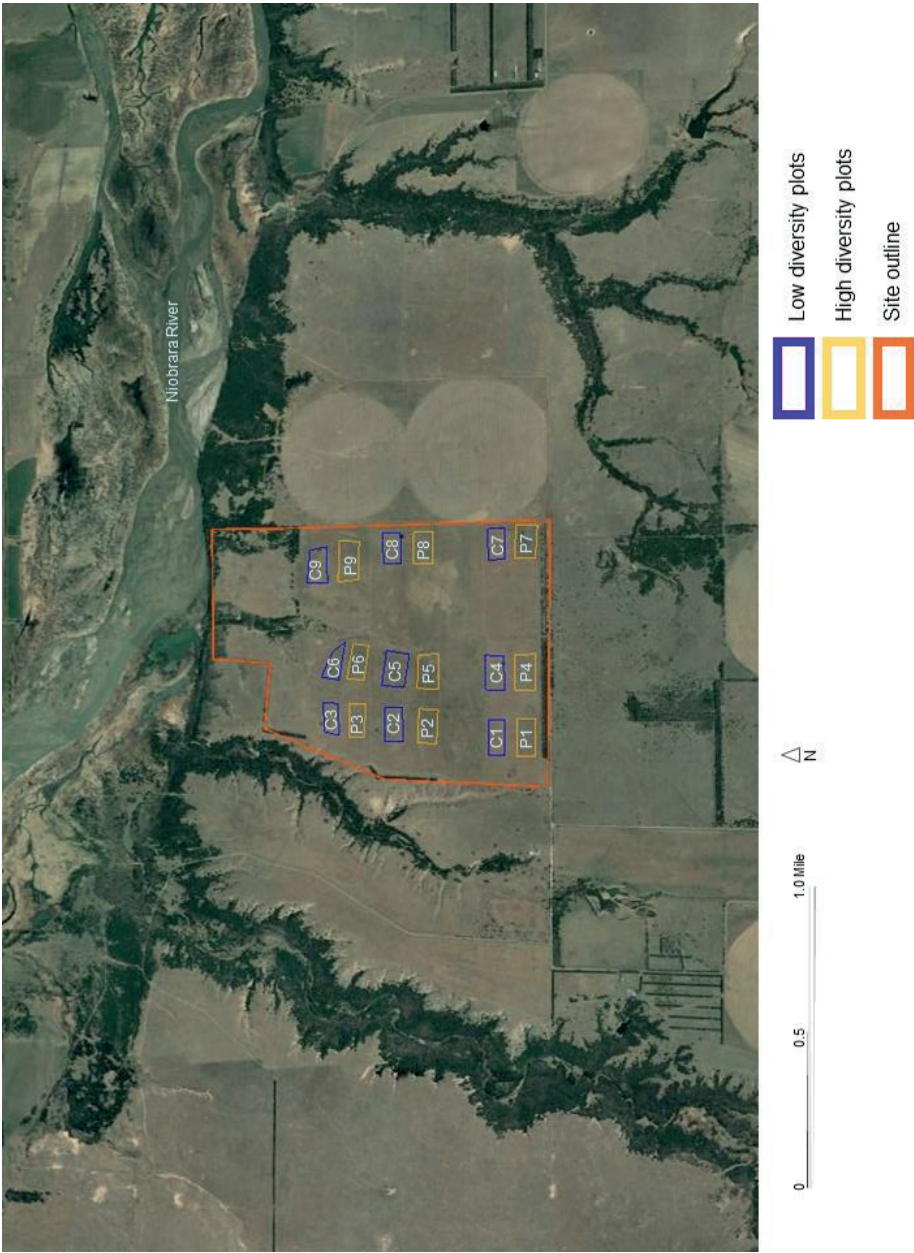
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APPENDIX A. AERIAL VIEW OF THE SOUTHEAST PRAIRIES BIOLOGICALLY UNIQUE LANDSCAPE AND THE LOCATION OF STUDY SITES WHERE WILD BEES WERE SAMPLED. Five study sites from each of Conservation Reserve Program (CRP (CP25); yellow), grazed pasture (orange), and haymeadow (also referred to as remnant prairie; purple) are shown. This focal study area encompasses approximately 84 square miles and spans between and around the villages of Steinauer and Table Rock, Nebraska in the counties of Pawnee, Richardson, and Johnson.



APPENDIX B. AERIAL VIEW OF THE HOLT COUNTY CRP STUDY LOCATION SHOWING THE POSITION OF HIGH AND LOW DIVERSITY CRP PLANTINGS FROM WHICH WILD BEES WERE SAMPLED. The site (outlined with orange) is located approximately three miles west of Highway 281 near the Spencer Dam, just on the south side of the Niobrara River. To the north is Boyd County, Nebraska. The nine high diversity plantings (yellow) were pollinator CRP seed mixes (CP42) and the low diversity plantings (blue) were CP25 mixes. Each plot measured approximately 185m by 90m, resulting in approximately four-acre designated plantings.



APPENDIX C. AERIAL VIEW OF THE PLATTE PRAIRIES STUDY LOCATION SHOWING PAIRS OF REMNANT AND RESTORED PRAIRIE SITES FROM WHICH WILD BEES WERE SAMPLED. Sites is owned and managed by The Nature Conservancy except for 'JR', which is a private property that abuts the TNC properties and was used with landowner permission. Prairie remnants are outlined in yellow and the restorations in blue. The sites are located just over six miles from Wood River in Hall County, Nebraska on the south side of the Platte River and I-80 on Highway 11. This study location lies within the Central Platte River ecosystem. Adjacent sites were paired for analysis: JR/99R. WDP/WDR. SH/PV. EDP/97R.

Species are listed by family and abundances are given for CRP, grazed pasture (PAS) and haymeadow (PRA) habitats for early- (D1), mid- (D2), and late-season (D3) flight periods. A grand total for the two years of collections is also listed.

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APPENDIX D (continued)

Species per family	CRP			PAS			PRA			Grand Total
	D1	D2	D3	D1	D2	D3	D1	D2	D3	
Megachilidae										
<i>Anthidiellum notatum</i>	-	1	-	-	-	1	1	-	-	3
<i>Coelioxys modesta</i>	1	-	-	-	-	-	-	-	-	1
<i>Coelioxys moesta</i>	1	-	-	-	-	-	-	-	-	1
<i>Coelioxys octodentata</i>	1	1	2	2	-	-	-	-	2	8
<i>Dianthidium curvatum</i>	-	-	-	-	1	4	1	-	1	7
<i>Heriades sp.**</i>	2	2	-	1	-	-	-	-	-	5
<i>Hoplitis pilosifrons</i>	11	1	-	4	-	-	2	-	-	18
<i>Megachile brevis</i>	3	6	4	6	2	1	2	6	4	34
<i>Megachile fortis</i>	-	1	2	-	-	3	-	-	1	7
<i>Megachile montivaga</i>	6	19	7	8	7	4	12	3	-	66
<i>Megachile parallela</i>	-	-	1	-	1	1	-	-	-	3
<i>Megachile sculpturalis</i>	-	-	-	1	-	-	-	-	-	1
<i>Megachile texana</i>	-	2	-	-	-	-	2	-	1	5
<i>Osmia subfasciata</i>	1	-	-	-	-	-	-	-	-	1
Total per flight period	158	812	674	1050	497	507	1452	727	710	8016
per habitat type	7									

**Agapostemon angelicus* and *Agapostemon texanus* are indistinguishable west of the Mississippi River and so these species are considered collectively under *A. angelicus*

**This species is unconfirmed as either *Heriades leavitti* or *H. veriolosa*, and is thusly considered *Heriades sp.*

APPENDIX E. SPECIES AND ABUNDANCES OF WILD BEES COLLECTED FROM HIGH AND LOW DIVERSITY CRP PLANTINGS FROM HOLT COUNTY, NEBRASKA IN EARLY-, MID- AND LATE-SEASON. Species are listed by family and abundances are summed between the two sampling years over early- (D1), mid- (D2), and late-season (D3) flight periods.

Species per family	High			Low			Grand Total
	D1	D2	D3	D1	D2	D3	
Andrenidae							
<i>Protandrena cockerelli</i>	-	1	-	-	-	-	1
Apidae							
<i>Anthophora bomboides</i>	-	1	-	-	2	-	3
<i>Anthophora occidentalis</i>	-	1	1	-	1	-	3
<i>Anthophora walshii</i>	-	4	5	-	-	8	17
<i>Apis mellifera</i>	13	5	-	16	10	1	45
<i>Bombus auricomus</i>	2	-	-	-	-	-	2
<i>Bombus bimaculatus</i>	-	-	-	2	-	-	2
<i>Bombus griseocollis</i>	-	-	-	-	-	1	1
<i>Bombus impatiens</i>	-	-	-	1	-	-	1
<i>Bombus pensylvanicus</i>	8	3	9	7	-	5	32
<i>Diadasia enavata</i>	-	1	-	-	1	3	5
<i>Eucera hamata</i>	62	33	-	70	59	-	224
<i>Melissodes agilis</i>	-	3	-	8	-	1	12
<i>Melissodes coloradensis</i>	-	-	1	-	-	15	16
<i>Melissodes comptoides</i>	-	5	-	-	7	35	47
<i>Melissodes coreopsis</i>	-	3	-	-	-	-	3
<i>Melissodes sp.</i>	5	2	795	15	4	414	1235
<i>Melissodes trinodis</i>	-	-	50	-	-	-	50
<i>Peponapis pruinosa</i>	-	-	-	-	1	-	1
<i>Svastra atripes</i>	-	-	5	-	-	17	22
<i>Svastra obliqua</i>	-	-	8	-	1	5	14
<i>Triepeolus sp.</i>	-	-	2	-	-	-	2
Halictidae							
<i>Agapostemon angelicus*</i>	12	-	5	28	3	9	57
<i>Agapostemon femoratus</i>	-	1	7	-	-	-	8
<i>Agapostemon virescens</i>	26	1	55	17	10	128	237
<i>Augochloropsis metallica</i>	1	-	-	3	2	-	6
<i>Augochoropsis sumptuosa</i>	7	6	-	5	3	1	22
<i>Halictus ligatus</i>	-	1	-	-	-	1	2
<i>Halictus parallelus</i>	4	-	9	8	1	1	23
<i>Halictus rubicundus</i>	-	1	-	2	-	-	3
<i>Lasioglossum sp.</i>	38	4	47	34	19	28	170
<i>Sphecodes sp.</i>	13	-	53	15	-	23	104

APPENDIX E (continued).							
Species per family	High			Low			Grand Total
	D1	D2	D3	D1	D2	D3	
Megachilidae							
<i>Hoplitis pilosifrons</i>	1	-	-	-	-	-	1
<i>Megachile montivaga</i>	-	4	-	-	-	-	4
Total per flight period per planting type	192	80	1052	231	124	696	2375

**Agapostemon angelicus* and *Agapostemon texanus* are indistinguishable west of the Mississippi River and so these species are considered collectively under *A. angelicus*

APPENDIX F. WILD BEE ABUNDANCES FOR PRAIRIE REMNANTS AND PRAIRIE RESTORATIONS WITHIN THE PLATTE PRAIRIES IN EARLY-, MID-, AND LATE-SEASON. Species are listed by family and abundances of bees collected with blue vane traps within early- (D1), mid- (D2), and late-season (D3) flight periods are given, as well as the grand total for the Platte Prairies study location summed across habitat types and flight periods.

Species per family	Remnants			Restorations			Grand
	D1	D2	D3	D1	D2	D3	Total
Andrenidae							
<i>Andrena commoda</i>	3	-	-	-	2	-	5
<i>Perdita pallida</i>	-	1	-	-	-	-	1
<i>Perdita sp. 1</i>	-	-	-	1	-	-	1
<i>Pseudopanurgus sp.</i>	-	-	-	-	1	-	1
Apidae							
<i>Anthophora bomboides</i>	-	-	1	1	-	-	2
<i>Anthophora walshii</i>	21	8	4	31	9	17	90
<i>Bombus auricomus</i>	1	-	4	3	-	6	14
<i>Bombus bimaculatus</i>	-	-	2	-	-	-	2
<i>Bombus griseocollis</i>	2	-	-	1	-	-	3
<i>Bombus impatiens</i>	-	-	-	2	-	1	3
<i>Bombus pensylvanicus</i>	24	6	26	5	8	11	80
<i>Ceratina dupla</i>	-	-	-	1	-	-	1
<i>Ceratina sp. 1</i>	-	-	-	10	-	-	10
<i>Diadasia enavata</i>	5	31	175	3	388	11	613
<i>Diadasia rinconis</i>	-	1	-	-	2	-	3
<i>Diadasia sp. 1</i>	-	-	-	-	9	-	9
<i>Dieunomia triangulifera</i>	1	-	-	-	-	-	1
<i>Epeolus sp.</i>	-	-	-	-	1	-	1
<i>Eucera hamata</i>	18	1	-	11	2	-	32
<i>Melissodes agilis</i>	21	15	28	7	12	26	109
<i>Melissodes bimaculata</i>	-	-	1	-	-	5	6
<i>Melissodes boltoniae</i>	-	10	1	-	3	8	22
<i>Melissodes communis</i>	-	8	5	-	10	4	27
<i>Melissodes comptoides</i>	3	6	8	2	11	5	35
<i>Melissodes desponsa</i>	-	-	8	-	-	14	22
<i>Melissodes nivea</i>	-	-	-	-	-	8	8
<i>Melissodes trinodis</i>	7	28	160	-	31	434	660
<i>Melitoma grisella</i>	-	-	-	-	-	1	1
<i>Peponapis pruinosa</i>	-	1	-	-	-	-	1
<i>Svastra atripes</i>	-	-	-	-	-	1	1
<i>Svastra obliqua</i>	-	2	5	-	-	16	23

APPENDIX F (continued).							
Species per family	Remnants			Restorations			Grand Total
	D1	D2	D3	D1	D2	D3	
Colletidae							
<i>Colletes eulophi</i>	-	1	-	-	-	3	4
Halictidae							
<i>Agapostemon angelicus</i> *	6	8	1	1	17	2	35
<i>Agapostemon sericeus</i>	10	-	-	8	1	-	19
<i>Agapostemon virescens</i>	24	4	1	14	10	-	53
<i>Augochlora pura</i>	6	-	-	1	-	1	8
<i>Augochlorella aurata</i>	16	1	1	3	1	4	26
<i>Augochloropsis metallica</i>	-	-	-	-	2	-	2
<i>Augochoropsis sumptuosa</i>	4	7	-	18	1	-	30
<i>Halictus ligatus</i>	5	3	3	-	1	12	24
<i>Halictus parallelus</i>	13	2	-	1	4	-	20
<i>Halictus rubicundus</i>	1	-	-	2	1	-	4
<i>Lasioglossum nymphaea</i>	5	-	-	5	-	1	11
<i>Lasioglossum</i> (v. <i>callidum</i>)	3	-	-	-	-	1	4
<i>Lasioglossum</i> sp. 1	-	-	-	6	1	-	7
<i>Lasioglossum</i> sp. 2	66	1	6	66	3	20	162
<i>Lasioglossum</i> sp. 3	1	1	-	1	-	7	10
<i>Sphecodes</i> spp.	16	3	1	13	3	18	54
Megachilidae							
<i>Coelioxys</i> sp.	1	-	-	1	-	-	2
<i>Heriades</i> sp. 1	6	-	-	-	-	-	6
<i>Hoplitis</i> sp.	9	-	-	4	-	-	13
<i>Megachile brevis</i>	-	1	-	-	-	-	1
<i>Megachile montivaga</i>	2	2	2	-	2	3	11
<i>Megachile</i> sp.	1	-	-	1	-	-	2
<i>Megachile texana</i>	-	1	-	1	-	-	2
Total per flight period per planting type	301	153	443	224	536	640	2297

**Agapostemon angelicus* and *Agapostemon texanus* are indistinguishable west of the Mississippi River and so these species are considered collectively under *A. angelicus*.

APPENDIX G: CLASSIFICATION OF WILD BEES FROM THE SOUTHEAST PRAIRIES BIOLOGICALLY UNIQUE LANDSCAPE INTO FUNCTIONAL GUILDS BY ASSIGNED FUNCTIONAL TRAITS. Species' functional traits were used to categorize wild bees into functional guilds. Species are listed by family and the assigned modalities for the traits of sociality, nesting strategy, foraging capacity, body size, and floral specificity are given. The functional guilds into which species were ultimately placed in cluster analysis are listed in the final column.

Species	Size (mm)	Foraging Range (m)	Sociality	Nesting Strategy	Specificity	Functional Guild
Andrenidae						
<i>Andrena commoda</i>	13-16 (13)	400-800	Solitary	Ground (blw)	Polylectic	Gnd.Ply (9)
<i>Andrena cressnii</i>	9-12 (10)	250-400	Solitary	Ground (blw)	Polylectic	SM.Sol.Gnd (1)
<i>Calliopsis andreniformis</i>	≤ 8 (7)	≤ 250	Solitary	Ground (blw)	Polylectic	Gnd.Ply (9)
<i>Protandrena bancrofti</i>	≤ 8 (8)	≤ 250	Solitary	Ground (blw)	Polylectic	Gnd.Ply (9)
Apidae						
<i>Anthophora abrupta</i>	13-16 (16)	400-800	Solitary	Ground (blw)	Polylectic	Gnd.Ply (9)
<i>Anthophora bomboidea</i>	13-16 (14.5)	400-800	Solitary	Ground (blw)	Polylectic	Gnd.Ply (9)
<i>Anthophora montana</i>	13-16 (16)	400-800	Solitary	Ground (blw)	Polylectic	Gnd.Ply (9)
<i>Anthophora occidentalis</i>	13-16 (16)	400-800	Solitary	Ground (blw)	Polylectic	Gnd.Ply (9)
<i>Anthophora walshii</i>	13-16 (16)	400-800	Solitary	Ground (blw)	Oligolectic	Sol.Gnd.Olg (3)
<i>Anthophora asteris</i>	≤ 8 (6.5)	≤ 250	Solitary	Ground (blw)	Polylectic	Gnd.Ply (9)
<i>Apis mellifera</i>	13-16 (14)	>1200	Social (lg)	Cavity (abv/blw)	Polylectic	Lg.Soc.LDF (4)
<i>Bombus auricomus</i>	17-20 (20)	800-1200	Social (lg)	Cavity (abv/blw)	Polylectic	Lg.Soc.LDF (4)
<i>Bombus bimaculatus</i>	17-20 (18)	800-1200	Social (lg)	Cavity (abv/blw)	Polylectic	Lg.Soc.LDF (4)
<i>Bombus fervidus</i>	17-20 (20)	800-1200	Social (lg)	Cavity (abv/blw)	Polylectic	Lg.Soc.LDF (4)
<i>Bombus fratrurnus</i>	21-27 (27)	>1200	Social (lg)	Cavity (abv/blw)	Polylectic	Lg.Soc.LDF (4)

APPENDIX G (continued).

Species	Size (mm)	Foraging Range (m)	Sociality	Nesting Strategy	Specificity	Functional Guild
Apidae continued						
<i>Bombus griseocollis</i>	17-20 (20)	800-1200	Social (lg)	Cavity (abv/bfw)	Polylectic	Lg.Soc.LDF (4)
<i>Bombus impatiens</i>	17-20 (18)	800-1200	Social (lg)	Cavity (abv/bfw)	Polylectic	Lg.Soc.LDF (4)
<i>Bombus pensylvanicus</i>	21-27 (22)	>1200	Social (lg)	Cavity (abv/bfw)	Polylectic	Lg.Soc.LDF (4)
<i>Ceratina calcarata</i>	≤ 8 (8)	≤ 250	Solitary	Wood (abv)	Polylectic	SM.Sol.Wd (2)
<i>Diadasia enavata</i>	21-27 (26)	>1200	Solitary	Ground (bw)	Oligolectic	Sol.Gnd.Olg (3)
<i>Diadasia rinconis</i>	9-12 (12)	250-400	Solitary	Ground (bw)	Oligolectic	Sol.Gnd.Olg (3)
<i>Eucera hamata</i>	17-20 (17)	800-1200	Solitary	Ground (bw)	Polylectic	Gnd.Ply (9)
<i>Habropoda morrisoni</i>	13-16 (16)	400-800	Solitary	Ground (bw)	Polylectic	Gnd.Ply (9)
<i>Melissodes agilis</i>	13-16 (15)	400-800	Solitary	Ground (bw)	Oligolectic	Sol.Gnd.Olg (3)
<i>Melissodes bimaculata</i>	13-16 (15)	400-800	Solitary	Ground (bw)	Polylectic	Gnd.Ply (9)
<i>Melissodes boltoniae</i>	13-16 (13)	400-800	Solitary	Ground (bw)	Polylectic	Gnd.Ply (9)
<i>Melissodes coloradensis</i>	13-16 (16)	400-800	Solitary	Ground (bw)	Polylectic	Gnd.Ply (9)
<i>Melissodes communis</i>	13-16 (14.5)	400-800	Solitary	Ground (bw)	Polylectic	Gnd.Ply (9)
<i>Melissodes comptaoides</i>	13-16 (13)	400-800	Solitary	Ground (bw)	Polylectic	Gnd.Ply (9)
<i>Melissodes coreopsis</i>	9-12 (11)	250-400	Solitary	Ground (bw)	Oligolectic	Sol.Gnd.Olg (3)
<i>Melissodes desponsa</i>	13-16 (13.5)	400-800	Solitary	Ground (bw)	Oligolectic	Sol.Gnd.Olg (3)
<i>Melissodes trinodis</i>	9-12 (12)	250-400	Solitary	Ground (bw)	Oligolectic	Sol.Gnd.Olg (3)
<i>Nomada affabilis</i>	9-12 (12)	250-400	Cleptoparasitic	Non-builder	Polylectic	SM.Clepto (6)
<i>Nomada texana</i>	9-12 (9)	250-400	Cleptoparasitic	Non-builder	Polylectic	SM.Clepto (6)

APPENDIX G (continued).

Species	Size (mm)	Foraging Range (m)	Sociality	Nesting Strategy	Specificity	Functional Guild
Apidae continued						
<i>Svastra atripes</i>	17-20 (20)	800-1200	Solitary	Ground (blw)	Oligolectic	Sol. Gnd. Olig (3)
<i>Svastra compta</i>	17-20 (18)	800-1200	Solitary	Ground (blw)	Oligolectic	Sol. Gnd. Olig (3)
<i>Svastra obliqua</i>	13-16 (16)	400-800	Solitary	Ground (blw)	Polylectic	Gnd. Ply (9)
<i>Triepoelus concavus</i>	13-16 (16)	400-800	Cleptoparasitic	Non-builder	Polylectic	ML. Clepto (5)
<i>Triepoelus lunatus</i>	13-16 (13)	400-800	Cleptoparasitic	Non-builder	Polylectic	ML. Clepto (5)
<i>Triepoelus sp. 2</i>	13-16 (14)	400-800	Cleptoparasitic	Non-builder	Polylectic	ML. Clepto (5)
<i>Triepoelus sp. 3</i>	13-16 (14)	400-800	Cleptoparasitic	Non-builder	Polylectic	ML. Clepto (5)
<i>Triepoelus sp. 4</i>	13-16 (14)	400-800	Cleptoparasitic	Non-builder	Polylectic	ML. Clepto (5)
<i>Triepoelus sp. 5</i>	13-16 (14)	400-800	Cleptoparasitic	Non-builder	Polylectic	ML. Clepto (5)
<i>Xenoglossa kansensis</i>	13-16 (16)	400-800	Solitary	Ground (blw)	Oligolectic	Sol. Gnd. Olig (3)
<i>Xenoglossa strenua</i>	17-20 (18)	800-1200	Solitary	Ground (blw)	Oligolectic	Sol. Gnd. Olig (3)
<i>Xeromelecta interrupta</i>	13-16 (16)	400-800	Cleptoparasitic	Non-builder	Polylectic	ML. Clepto (5)
<i>Xyllocopa virginica</i>	21-27 (23)	>1200	Social (lg)	Wood (abv)	Polylectic	Lg. Wd (10)
Colletidae						
<i>Colletes eulophi</i>	13-16 (14)	400-800	Solitary	Ground (blw)	Polylectic	Gnd. Ply (9)
Halictidae						
<i>Agapostemon angelicus</i> *	9-12 (11)	250-400	Solitary	Ground (blw)	Polylectic	SM. Sol. Gnd (1)
<i>Agapostemon sericeus</i>	9-12 (11)	250-400	Solitary	Ground (blw)	Polylectic	SM. Sol. Gnd (1)
<i>Agapostemon virescens</i>	9-12 (11)	250-400	Solitary	Ground (blw)	Polylectic	SM. Sol. Gnd (1)

APPENDIX G (continued).

Species	Size (mm)	Foraging Range (m)	Sociality	Nesting Strategy	Specificity	Functional Guild
Halictidae continued						
<i>Augochlora pura</i>	≤ 8 (8)	≤ 250	Solitary	Wood (abv)	Polylectic	SM.Sol.Wd (2)
<i>Augochlora aurata</i>	≤ 8 (5.5)	≤ 250	Solitary	Ground (blw)	Polylectic	Gnd.Ply (9)
<i>Augochlora persimilis</i>	≤ 8 (6)	≤ 250	Solitary	Ground (blw)	Polylectic	Gnd.Ply (9)
<i>Augochloropsis metallica</i>	9-12 (9)	250-400	Solitary	Ground (blw)	Polylectic	SM.Sol.Gnd (1)
<i>Augochloropsis sumptuosa</i>	9-12 (11)	250-400	Gregarious	Ground (blw)	Polylectic	SM.Sol.Gnd (1)
<i>Halictus confusus</i>	≤ 8 (7)	≤ 250	Social (sm)	Ground (blw)	Polylectic	Sm.Soc.MDF (8)
<i>Halictus ligatus</i>	9-12 (10)	250-400	Social (sm)	Ground (blw)	Polylectic	Sm.Soc.MDF (8)
<i>Halictus parallelus</i>	13-16 (13)	400-800	Social (sm)	Ground (blw)	Polylectic	Sm.Soc.MDF (8)
<i>Halictus rubicundus</i>	9-12 (11)	250-400	Social (sm)	Ground (blw)	Polylectic	Sm.Soc.MDF (8)
<i>Lasioglossum nr. cressonii</i>	≤ 8 (6.5)	≤ 250	Solitary	Ground (blw)	Polylectic	Gnd.Ply (9)
<i>Lasioglossum nymphaea</i>	≤ 8 (7)	≤ 250	Solitary	Ground (blw)	Oligolectic	Sol.Gnd.Olg (3)
<i>Lasioglossum sp. 1 (v. callidum)</i>	≤ 8 (6.5)	≤ 250	Solitary	Ground (blw)	Polylectic	Gnd.Ply (9)
<i>Lasioglossum sp. 2</i>	≤ 8 (6)	≤ 250	Solitary	Ground (blw)	Polylectic	Gnd.Ply (9)
<i>Lasioglossum sp. 3</i>	≤ 8 (6)	≤ 250	Solitary	Ground (blw)	Polylectic	Gnd.Ply (9)
<i>Nomia nortoni</i>	13-16 (16)	400-800	Solitary	Ground (blw)	Polylectic	Gnd.Ply (9)
Megachilidae						
<i>Anthidiellum notatum</i>	≤ 8 (8)	≤ 250	Solitary	Wood (abv)	Polylectic	SM.Sol.Wd (2)
<i>Coelioxys modesta</i>	13-16 (13)	400-800	Cleptoparasitic	Non-builder	Polylectic	ML.Clepto (5)

APPENDIX G (continued).

Species	Size (mm)	Foraging Range (m)	Sociality	Nesting Strategy	Specificity	Functional Guild
Megachilidae continued						
<i>Coelioxys moesta</i>	9-12 (12)	250-400	Cleptoparasitic	Non-builder	Polylectic	SM.Clepto (6)
<i>Coelioxys octodentata</i>	9-12 (12)	250-400	Cleptoparasitic	Non-builder	Polylectic	SM.Clepto (6)
<i>Dianthidium curvatum</i>	≤8 (7)	≤250	Solitary	Wood (abv)	Oligolectic	Sm.Wd.Olg (7)
<i>Heriades</i> spp. **	≤8 (7)	≤250	Solitary	Wood (abv)	Polylectic	SM.Sol.Wd (2)
<i>Hoplitis pilosifrons</i>	≤8 (8.5)	≤250	Solitary	Wood (abv)	Polylectic	SM.Sol.Wd (2)
<i>Megachile brevis</i>	9-12 (12)	250-400	Solitary	Wood (abv)	Polylectic	SM.Sol.Wd (2)
<i>Megachile fortis</i>	17-20 (18)	800-1200	Solitary	Wood (abv)	Polylectic	SM.Sol.Wd (2)
<i>Megachile montivaga</i>	13-16 (13)	400-800	Solitary	Wood (abv)	Polylectic	SM.Sol.Wd (2)
<i>Megachile parallela</i>	13-16 (14)	400-800	Solitary	Wood (abv)	Polylectic	SM.Sol.Wd (2)
<i>Megachile sculpturalis</i>	21-27 (25)	>1200	Solitary	Wood (abv)	Polylectic	Lg.Wd (10)
<i>Megachile texana</i>	13-16 (14)	400-800	Solitary	Wood (abv)	Polylectic	SM.Sol.Wd (2)
<i>Osmia subfasciata</i>	≤8 (8)	≤250	Solitary	Wood (abv)	Polylectic	SM.Sol.Wd (2)

Notes: Natural history and behavioral traits were determined from these sources. Only eusocial species with a queen as the only egg-laying female were categorized as social, gregarious species were considered solitary. Social species were further categorized into large (lg) and small (sm) social bees. Nest building species were also more broadly categorized as above (abv) or below (blw) ground nesters. Floral specificity was only categorized as generalist (polylectic) or oligolectic (some known specificity or preference). Monoleptic species were grouped with oligoleges. Functional guilds included large social long-distance foragers (Lg.Soc.LDF), small social moderate-distance foragers (Sm.Soc.MDF), solitary ground-nesting oligoleges (Sol.Gnd.Olg), ground-nesting polyleges (Gnd.Ply), small cleptoparasites (SM.Clepto), medium and large cleptoparasites (ML.Clepto), large wood-nesters (Lg.Wd), small solitary wood-nesters (SM.Sol.Wd), and small wood-nesting oligoleges (Sm.Wd.Olg). The numbers in parentheses indicate the number of species included within each functional guild.

* *Agapostemon angelicus* and *A. texanus* are considered collectively under *A. angelicus* because the females of these species are morphologically indistinguishable west of the Mississippi River.

** This species is unconfirmed as either *Heriades leavittii* or *H. variolosa*, and is thusly considered *Heriades* spp.

APPENDIX H. BLOOMING FORB ABUNDANCES FOR HAYMEADOW, GRAZED PASTURE, AND CRP STUDY SITES IN THE SOUTHEAST PRAIRIES BIOLOGICALLY UNIQUE LANDSCAPE. The number of blooming stems counted for each of the three grassland types (CRP, grazed pasture (PAS), and remnant prairie (PRA) in the Southeast Prairies BUL is listed, as well as the mean and standard error per habitat type.

Species (Listed per family)	Total blooming stems			Mean blooming stems (s.e.)		
	CRP	PAS	PRA	CRP	PAS	PRA
Acanthaceae						
<i>Ruellia humilis</i>	4	52	35	0.8 (0.8)	10.4 (6.87)	7 (3.11)
<i>Ruellia strepens</i>	-	1	4	0 (0)	0.2 (0.2)	0.8 (0.8)
Asclepiadaceae						
<i>Asclepias asperula</i>	-	-	1	0 (0)	0 (0)	0.2 (0.2)
<i>Asclepias fascicularis</i>	-	1	-	0 (0)	0.2 (0.2)	0 (0)
<i>Asclepias hirtella</i>	-	-	2	0 (0)	0 (0)	0.4 (0.4)
<i>Asclepias syriaca</i>	36	-	-	7.2 (7.2)	0 (0)	0 (0)
<i>Asclepias tuberosa</i>	-	-	27	0 (0)	0 (0)	5.4 (2.77)
Asteraceae						
<i>Achillea millefolium</i>	-	211	851	0 (0)	42.2 (23.30)	170.2 (51.84)
<i>Brickellia eupatorioides</i>	92	11	-	18.4 (14.53)	2.2 (1.96)	0 (0)
<i>Carduus nutans</i>	5	1119	66	1 (0.63)	223.8 (163.87)	13.2 (6.32)
<i>Cichorium intybus</i>	-	2	-	0 (0)	0.4 (0.4)	0 (0)
<i>Cirsium flodmanii</i>	-	5	3	0 (0)	1 (0.77)	0.6 (0.24)
<i>Coreopsis palmata</i>	-	-	31	0 (0)	0 (0)	6.2 (4.84)
<i>Echinacea purpurea</i>	-	-	2	0 (0)	0 (0)	0.4 (0.4)
<i>Erigeron spp.</i>	134	499	2352	26.8 (9.32)	99.8 (73.10)	470.4 (131.21)
<i>Gaillardia pulchella</i>	-	-	2	0 (0)	0 (0)	0.4 (0.4)
<i>Helianthus annuus</i>	12	-	-	2.4 (2.16)	0 (0)	0 (0)
<i>Helianthus grosseserratus</i>	2	-	1	0.4 (0.4)	0 (0)	0.2 (0.2)
<i>Hieracium longipilum</i>	-	-	18	0 (0)	0 (0)	3.6 (2.91)

APPENDIX H (continued).

Species (Listed per family)	Total blooming stems			Mean blooming stems (s.e.)		
	CRP	PAS	PRA	CRP	PAS	PRA
Asteraceae						
<i>Leucanthemum vulgare</i>	4	2	502	0.8 (0.49)	0.4 (0.4)	100.4 (43.14)
<i>Oligoneuron rigidum</i> *	15	1	-	3 (3)	0.2 (0.2)	0 (0)
<i>Ratibida columnifera</i>	75	7	-	15 (15)	1.4 (1.4)	0 (0)
<i>Rudbeckia hirta</i>	376	137	4525	75.2 (41.54)	27.4 (18.57)	905 (187.88)
<i>Silphium laciniatum</i>	-	-	253	0 (0)	0 (0)	50.6 (19.22)
<i>Solidago juncea</i>	-	-	1	0 (0)	0 (0)	0.2 (0.2)
<i>Solidago missouriensis</i>	-	-	4	0 (0)	0 (0)	0.8 (0.8)
<i>Symphotrichum ericoides</i>	1	8	137	0.2 (0.2)	1.6 (1.36)	27.4 (13.49)
<i>Taraxacum officinale</i>	-	8	-	0 (0)	1.6 (1.6)	0 (0)
<i>Tragopogon dubius</i>	-	1	-	0 (0)	0.2 (0.2)	0 (0)
<i>Vernonia baldwinii</i>	99	107	15	19.8 (15.44)	21.4 (9.93)	3 (1.82)
Caryophyllaceae						
<i>Dianthus armeria</i>	0	550	184	0 (0)	110 (91.50)	36.8 (22.88)
Clusiaceae						
<i>Hypericum perforatum</i>	12	7	10	2.4 (2.4)	1.4 (0.87)	2 (1.55)
Convolvulaceae						
<i>Calystegia sepium</i>	1	0	0	0.2 (0.2)	0 (0)	0 (0)
<i>Convolvulus arvensis</i>	721	13	0	144.2 (141.22)	2.6 (2.6)	0 (0)
Euphorbiaceae						
<i>Euphorbia corollata</i>	0	0	1149	0 (0)	0 (0)	229.8 (221.86)

APPENDIX H (continued).

Species (Listed per family)	Total blooming stems			Mean blooming stems (s.e.)		
	CRP	PAS	PRA	CRP	PAS	PRA
Fabaceae						
<i>Amorpha canescens</i>	0	0	312	0 (0)	0 (0)	62.4 (27.14)
<i>Astragalus canadensis</i>	0	0	1	0 (0)	0 (0)	0.2 (0.2)
<i>Chamaecrista fasciculata</i>	725	0	0	145 (86.51)	0 (0)	0 (0)
<i>Dalea candida</i>	173	1	1413	34.6 (34.6)	0.2 (0.2)	282.6 (142.05)
<i>Dalea purpurea</i>	52	0	269	10.4 (9.17)	0 (0)	53.8 (38.09)
<i>Desmodium illinoense</i>	6	0	18	1.2 (1.2)	0 (0)	3.6 (2.638)
<i>Lotus corniculatus</i>	0	0	78	0 (0)	0 (0)	15.6 (15.6)
<i>Medicago sativa</i>	37	16	45	7.4 (4.94)	3.2 (3.2)	9 (9)
<i>Melilotus alba</i>	1044	85	0	208.8 (146.37)	17 (16.01)	0 (0)
<i>Melilotus officinalis</i>	1921	595	551	384.2 (171.18)	119 (44.51)	110.2 (109.20)
<i>Mimosa microphylla/nuttallii</i>	0	1	1	0 (0)	0.2 (0.2)	0.2 (0.2)
<i>Psoraleidium tenuiflorum</i>	0	0	3771	0 (0)	0 (0)	754.2 (298.89)
<i>Trifolium campestre</i>	2	83	111	0.4 (0.24)	16.6 (16.6)	22.2 (14.93)
<i>Trifolium pratense</i>	208	712	6943	41.6 (22.17)	142.4 (121.27)	1388.6 (559.98)
<i>Trifolium repens</i>	0	9	0	0 (0)	1.8 (1.8)	0 (0)
Lamiaceae						
<i>Salvia officinalis</i>	0	0	8	0 (0)	0 (0)	1.6 (0.68)
Linaceae						
<i>Linum sulcatum</i>	0	0	93	0 (0)	0 (0)	18.6 (8.99)
Onagraceae						
<i>Gaura parviflora</i>	0	1	2	0 (0)	0.2 (0.2)	0.4 (0.24)
<i>Oenothera biennis</i>	0	0	22	0 (0)	0 (0)	4.4 (4.4)
Rhamnaceae						
<i>Ceanothus americanus</i>	0	0	161	0 (0)	0 (0)	32.2 (18.47)

APPENDIX H (continued).

Species (Listed per family)	Total blooming stems			Mean blooming stems (s.e.)		
	CRP	PAS	PRA	CRP	PAS	PRA
Rosaceae						
<i>Potentilla recta</i>	0	0	24	0 (0)	0 (0)	4.8 (2.75)
Scrophulariaceae						
<i>Penstemon angustifolius</i>	0	0	2	0 (0)	0 (0)	0.4 (0.4)
<i>Verbascum blattaria</i>	0	34	2	0 (0)	6.8 (6.30)	0.4 (0.4)
<i>Verbascum thapsus</i>	2	3	0	0.4 (0.4)	0.6 (0.6)	0 (0)
Solanaceae						
<i>Physalis heterophylla</i>	41	7	0	8.2 (4.94)	1.4 (0.98)	0 (0)
<i>Solanum carolinense</i>	20	32	0	4 (3.75)	6.4 (2.32)	0 (0)
Verbenaceae						
<i>Verbena stricta</i>	11	455	0	2.2 (1.02)	91 (43.99)	0 (0)

* *Oligoneuron rigidum* is a recent classification of stiff goldenrod, formerly *Solidago rigida*

APPENDIX I. POLLEN PROFILES OF WILD BEES COLLECTED FROM THREE HABITAT TYPES IN THE SOUTHEAST PRAIRIES BIOLOGICALLY UNIQUE LANDSCAPE. The pollen profiles of wild bees collected from haymeadow (PRA), grazed pasture (PAS), and CRP habitats are listed by growth form and plant family. Pollen grains were summed across bees and study sites for each habitat type. Total across habitats are also given. Pollen concentrations are the means of pollen grains per bee per sample which was processed via acetolysis.

Growth form	Pollen type	CRP	PAS	PRA	Total
Woody (trees and shrubs)	Anacardiaceae				
	<i>Rhus</i>	3	-	2	5
	Asteraceae				
	<i>Baccharis</i>	55	95	3	153
	Betulaceae				
	<i>Betula</i>	-	-	53	53
	Caprifoliaceae				
	Caprifoliaceae	-	-	11	11
	<i>Viburnum</i>	7	13	-	20
	Cornaceae				
	<i>Cornus</i>	-	3	-	3
	Fabaceae				
	<i>Robinia</i>	50	-	195	245
	Pinaceae				
	<i>Pinus</i>	2	-	-	2
	Rhamnaceae				
	<i>Ceanothus</i>	-	-	46	46
	Rhamnaceae	2	-	-	2
	Rosaceae				
	<i>Potentilla</i>	-	-	7	7
	<i>Rosa</i>	-	-	5	5
	<i>Rosa arkansana</i>	-	3	-	3
	Rosaceae	3	12	3	18
	Salicaceae				
	<i>Salix</i>	1	-	-	1
Herbaceous (forbs)	Apiaceae				
	Apiaceae	0	0	3	3
	<i>Bupleurum</i>	0	2	0	2

Appendix I (continued).

Growth form	Pollen type	CRP	PAS	PRA	Total
Herbaceous (forbs)	Asteraceae				
	<i>Achillea millefolium</i>	6	80	1	87
	<i>Ambrosia</i>	18	0	4	22
	Asteraceae (LS)*	10	0	45	55
	<i>Carduus</i>	34	77	50	161
	Chichorieae (Lactuceae)	0	4	1	5
	<i>Erigeron</i>	4	4	2	10
	<i>Eupatorium</i> c.f.	15	0	68	83
	<i>Helianthus</i>	0	0	101	101
	<i>Taraxacum</i>	1	0	2	3
	Boraginaceae				
	<i>Echium vulgare</i>	0	20	0	20
	Brassicaceae				
	Brassicaceae	90	0	44	134
	Caryophyllaceae				
	<i>Dianthus</i>	1	0	0	1
	Cucurbitaceae				
	<i>Cucurbita</i>	2	0	0	2
	Euphorbiaceae				
	<i>Euphorbia</i>	0	3	1	4
	Fabaceae				
	<i>Amorpha</i>	9	0	0	9
	<i>Dalea</i>	7	6	0	13
	Fabaceae	41	28	6	75
	Leguminosae	0	0	12	12
	<i>Medicago</i>	0	2	14	16
	<i>Melilotus</i>	4	37	14	55
	<i>Mimosa</i>	0	0	50	50
	<i>Trifolium</i> sp.	271	126	410	807
	<i>Trifolium pratense</i>	87	0	52	139
	Lamiaceae				
	Lamiaceae	0	0	2	2
	Saxifragaceae				
	Saxifragaceae	1	0	9	10

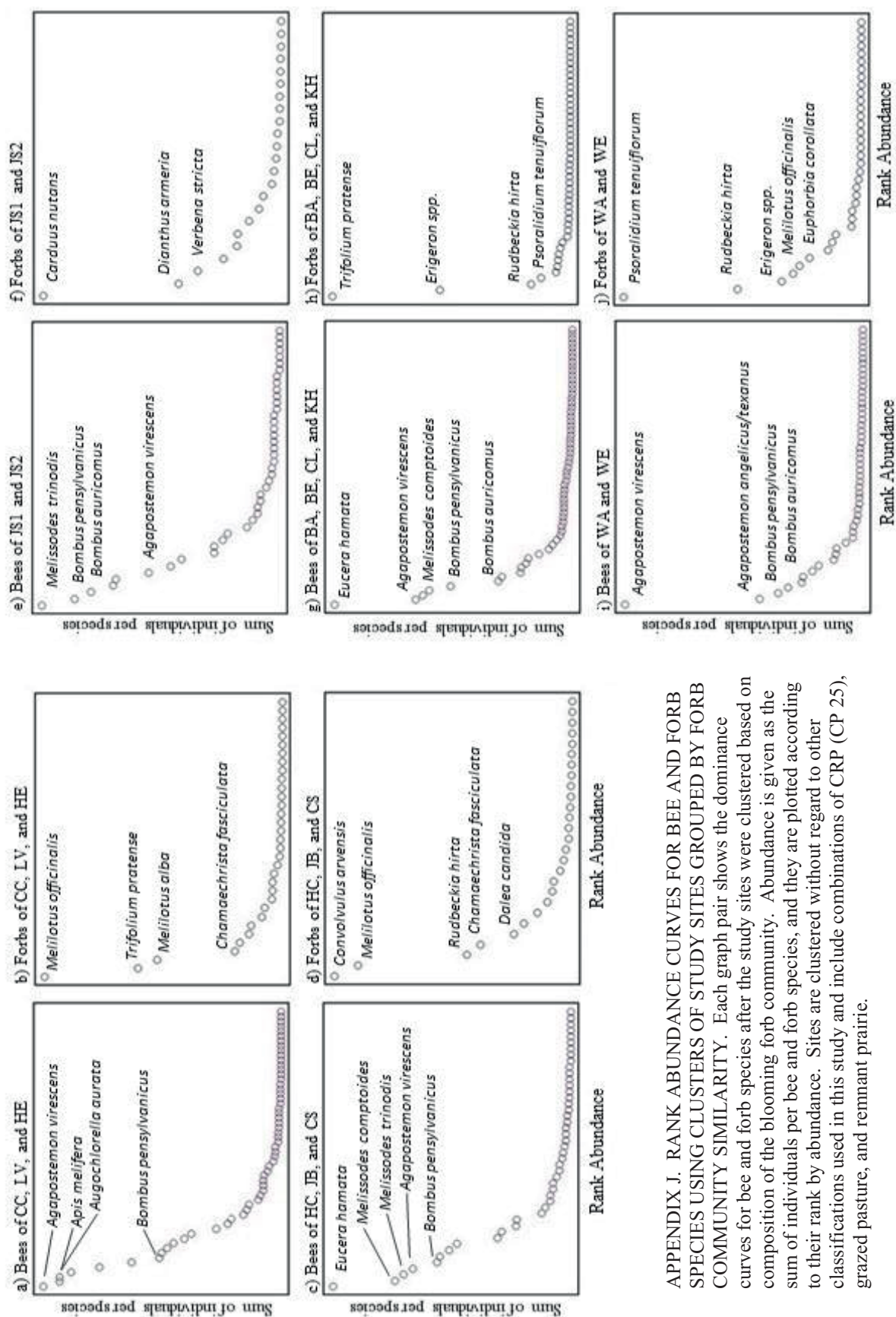
Appendix I (continued).

Growth form	Pollen type	CRP	PAS	PRA	Total
Herbaceous (forbs)	Scrophulariaceae				
	Scrophulariaceae	2	0	0	2
	Solanaceae				
	Solanaceae	57	46	3	106
	Solanum	0	23	6	29
Gramminoid (grasses)	Violaceae				
	Violaceae	0	0	6	6
	Poaceae				
	Poaceae	8	0	5	13
	<i>Zea mays</i>	3	0	0	3
Undetermined**	Unidentifiable	24	0	1	25
	Unknown	16	24	271	311
Totals	Total Pollen	834	608	1508	2950
	Lycopodium	562	415	295	1272
	Pollen Concentration***	21908.3	8144	194150	86216.9

* Asteraceae (LS) refers to large spore pollen grains within the family Asteraceae

** 'Unidentifiable' pollen grains were damaged or otherwise observed in a state in which more specific identification of the pollen type was not possible. 'Unknown' describes pollen grains which were observed in good condition, but for which a more specific identity was not known from the reference pollen library or expertise.

***Pollen concentration per sample/bee specimen is calculated as the ratio of pollen grains counted to Lycopodium spores counted, multiplied by the number of Lycopodium spores added to each solution ($(\# \text{ pg}_{\text{counted}} / \# \text{ Lsp}_{\text{counted}}) * \# \text{ Lsp}_{\text{added}}$). Mean pollen concentrations per bee per habitat are given.



APPENDIX J. RANK ABUNDANCE CURVES FOR BEE AND FORB SPECIES USING CLUSTERS OF STUDY SITES GROUPED BY FORB COMMUNITY SIMILARITY. Each graph pair shows the dominance curves for bee and forb species after the study sites were clustered based on composition of the blooming forb community. Abundance is given as the sum of individuals per bee and forb species, and they are plotted according to their rank by abundance. Sites are clustered without regard to other classifications used in this study and include combinations of CRP (CP 25), grazed pasture, and remnant prairie.

APPENDIX K. RESULTS OF INDICATOR SPECIES ANALYSIS ON BEES AND FORBS AFTER CLUSTERING STUDY SITES BY SIMILARITY IN SPECIES

COMPOSITION. Results of Monte Carlo test of significance on indicator values for wild bees and forbs in the Southeast Prairies BUL with study sites clustered by similarities in bee and forb species composition. Listed are the site clusters in which species are significantly abundant and constant, their indicator values (IV), the mean abundance and standard deviation, and the *p*-value.

Species	Site Cluster (max)	IV	Mean (s.d.)	<i>p</i> -value
Sites Clustered by Forb Species Composition				
<i>Agapostemon angelicus</i> *	WA, WE	46.2	35.8 (5.3)	0.0370
<i>Anthophora occidentalis</i>	CC, LV, HE	78.7	46.8 (16.8)	0.0394
<i>Megachile montivaga</i>	CC, LV, HE	43.8	33.5 (5.3)	0.0440
<i>Amorpha canescens</i>	WA, WE	75.9	36.6 (17.3)	0.0422
<i>Asclepias tuberosa</i>	WA, WE	75.4	32.0 (16.6)	0.0310
<i>Carduus nutans</i>	JS1, JS2	93.9	62.0 (17.7)	0.0048
<i>Cirsium flodmanii</i>	JS1, JS2	62.7	34.2 (14.3)	0.0514
<i>Melilotus alba</i>	CC, LV, HE	96.0	47.6 (19.5)	0.0044
<i>Mimosa microphylla</i>	WA, WE	90.0	41.0 (19.4)	0.0418
<i>Psoraleidum tenuiflorum</i>	WA, WE	82.0	37.4 (16.4)	0.0072
<i>Rudbeckia hirta</i>	WA, WE	94.7	40.1 (18.4)	0.0426
<i>Salvia officinalis</i>	WA, WE	76.9	30.5 (16.5)	0.0390
<i>Trifolium pratense</i>	BA, BE, CL, KH	79.3	44.3 (11.6)	0.0010
Sites Clustered by Bee Species Composition				
<i>Agapostemon virescens</i>	BA, HE, WA, WE	63.6	35.8 (6.6)	0.0002
<i>Anthophora abrupta</i>	KH, CL	100.0	31.1 (16.6)	0.0238
<i>Eucera hamata</i>	KH, CL	45.4	33.6 (5.3)	0.0232

APPENDIX K. continued...

Species	Site Cluster (max)	IV	Mean (s.d.)	<i>p</i> -value
Sites Clustered by Bee Species Composition				
<i>Melissodes comptoides</i>	KH, CL	34.8	27.8 (3.3)	0.0270
<i>Megachile brevis</i>	KH, CL	37.5	29.5 (3.8)	0.0234
<i>Xylocopa virginica</i>	KH, CL	40.5	30.4 (4.1)	0.0160
<i>Asclepias tuberosa</i>	BA, HE, WA, WE	75.0	31.6 (16.6)	0.0494
<i>Erigeron spp.</i>	KH, CL	80.2	63.9 (11.4)	0.0364
<i>Veronia baldwinii</i>	CC, JS1	80.8	48.5 (14.3)	0.0100

Notes: Habitat (max) indicates the habitat in which the maximum indicator value (IV) was observed. The *p*-values listed represent the proportion of 4999 randomized trials in a Monte Carlo simulation in which indicator values equal or exceed the observed indicator value. A small *p*-value indicates that a species is more abundant and constant than would be expected by chance.

**Agapostemon angelicus* and *A. texanus* are morphologically indistinguishable west of the Mississippi River and therefore, both species are included under the classification of *A. angelicus* in this study.

APPENDIX L. RESULTS OF SPEARMAN RANK CORRELATION ANALYSIS ON SIGNIFICANT BEE AND FORB SPECIES. Relevant bee and forb species were taken from Indicator Species Analysis on the prairie, pasture, and CRP habitats of the Southeast Prairies BUL. Spearman Rank Correlations were used to identify significant correlations between these species of bees and forbs. Listed for each pairing is the S statistic, p-value, and rho correlation coefficient. Significant correlations are indicated with boldface type, although after Holm-Sidak adjustments none of the correlations retained their significance.

Bee Species	Forb Species															
	<i>Achillea millefolium</i>	<i>Amorpha canescens</i>	<i>Ceanothus herbaceus</i>	<i>Dalea candida</i>	<i>Linum sulcatum</i>	<i>Potentilla recta</i>	<i>Psoraleum tenuiflorum</i>	<i>Rudbeckia hirta</i>	<i>Siphium laciniatum</i>	<i>Symphoricarum encades</i>	<i>Trifolium pratense</i>	<i>Verbena stricta</i>				
<i>Anthophora walsbyi</i>	-0.455 0.020	-0.184 0.369	-0.212 0.298	-0.143 0.486	-0.253 0.213	-0.086 0.675	-0.193 0.344	-0.260 0.199	-0.209 0.306	-0.221 0.278	-0.187 0.361	-0.125 0.543				
<i>Apis mellifera</i>	-0.414 0.036	-0.345 0.084	-0.110 0.594	-0.458 0.019	-0.112 0.586	-0.312 0.121	-0.359 0.072	-0.374 0.060	-0.155 0.450	-0.209 0.306	-0.206 0.312	0.081 0.694				
<i>Diadasia enervata</i>	-0.255 0.208	-0.046 0.824	-0.196 0.337	0.039 0.851	0.164 0.425	-0.392 0.048	-0.326 0.104	0.106 0.606	0.243 0.231	0.491 0.011	-0.168 0.412	0.161 0.433				
<i>Halictus ligatus</i>	-0.250 0.218	-0.091 0.658	-0.103 0.616	-0.223 0.273	-0.026 0.899	-0.319 0.112	-0.297 0.140	0.024 0.906	-0.067 0.746	-0.007 0.972	-0.018 0.929	0.126 0.541				
<i>Lasiglossum nymphaeaeum</i>	0.461 0.018	0.388 0.050	0.506 0.008	0.252 0.214	0.353 0.077	0.338 0.091	0.468 0.016	0.336 0.094	0.488 0.011	0.329 0.101	0.224 0.272	-0.256 0.207				
<i>Melissodes agilis</i>	-0.307 0.127	-0.234 0.250	-0.198 0.333	-0.297 0.140	-0.010 0.962	-0.533 0.005	-0.419 0.033	-0.248 0.223	-0.001 0.996	0.106 0.605	-0.449 0.021	0.311 0.122				
<i>Melissodes bimaculata</i>	-0.421 0.032	-0.167 0.414	-0.292 0.148	-0.144 0.483	0.072 0.728	-0.528 0.006	-0.432 0.027	-0.112 0.587	0.190 0.353	0.386 0.052	-0.270 0.183	0.282 0.162				
<i>Melissodes coloradensis</i>	-0.175 0.392	-0.058 0.778	-0.111 0.590	0.047 0.820	0.000 1.000	-0.235 0.248	-0.201 0.324	-0.005 0.983	-0.089 0.667	0.158 0.441	-0.394 0.046	0.120 0.558				
<i>Melissodes comptoides</i>	-0.278 0.169	-0.029 0.887	-0.057 0.780	-0.044 0.832	0.174 0.394	-0.418 0.034	-0.260 0.200	-0.069 0.738	0.178 0.386	0.347 0.083	-0.312 0.121	0.400 0.043				

APPENDIX M. SEASONAL DIFFERENCES IN WILD BEE AND BLOOMING FORB COMMUNITIES IN THE SOUTHEAST PRAIRIES BIOLOGICALLY UNIQUE LANDSCAPE. MRPP was used to determine whether the species composition wild bee and blooming forb species compositions between the 2012 and 2014 sampling seasons. Listed are the within-group agreement (A) and p -values with a significance level of $\alpha \leq 0.05$ for each community overall between study seasons, as well as for each site type (CRP, grazed pasture PAS), and remnant prairie (PRA)) between study seasons 2012 and 2014. Significant differences are shown in boldface type.

Community Comparisons	Within-Group Agreement (A)	Probability of \leq Delta (p)
Bee community (all study sites)	0.0726	0.0001
Forb community (all study sites)	-0.0023	0.5067
Pairwise Comparisons (Bees)		
▪ CRP 2012—CRP 2014	0.0536	0.0673
▪ PAS 2012—PAS 2014	-0.0260	0.7748
▪ PRA 2012—PRA 2014	0.1322	0.0044
Pairwise Comparisons (Forbs)		
▪ CRP 2012—CRP 2014	0.0074	0.3800
▪ PAS 2012—PAS 2014	0.0008	0.4397
▪ PRA 2012—PRA 2014	0.0351	0.1694

Notes: Adjustments were made for multiple comparisons using the Holm-Sidak method.

Summary: Overall, there were no differences in the species composition of the blooming forb community ($A = -0.0023$, $p = 0.5067$), neither between seasons for all study sites collectively, nor within CRP, pasture, or prairie sites between seasons. The composition of the wild bee community, however, differed between the 2012 and 2014 seasons ($A = 0.0726$, $p = 0.0001$), specifically the bees collected from prairie ($A = 0.0351$, $p = 0.0044$).

APPENDIX N. RESULTS OF INDICATOR SPECIES ANALYSES TO IDENTIFY SEASONAL SPECIFICITY OF WILD BEES AND BLOOMING FORBS IN THE SOUTHEAST PRAIRIES BIOLOGICALLY UNIQUE LANDSCAPE. Indicator species analyses were used to determine which species of bees and forbs were significantly more abundant in either the 2012 or 2014 season. Listed for each is the indicator value (IV), mean abundance and standard deviation, and *p*-value provided by Monte Carlo test of significance on indicator values. Habitat indicates CRP, pasture (PAS) or prairie (PRA), and season.

Species	Habitat (max)	IV	Mean (s.d.)	<i>p</i> -value
Bees				
<i>Augochlorella pura</i>	PRA 14	60.0	22.5 (12.8)	0.0234
<i>Bombus fervidus</i>	PAS 14	50.0	19.6 (13.2)	0.0206
<i>Bombus grisiocolis</i>	CRP 12	47.1	27.3 (8.35)	0.0276
<i>Melissodes agilis</i>	CRP 12	38.7	25.7 (6.19)	0.0326
<i>Melissodes bimaculata</i>	CRP 12	46.9	29.6 (5.69)	0.0070
<i>Melissodes coloradensis</i>	CRP 12	60.0	24.1 (10.1)	0.0022
<i>Melissodes communis</i>	CRP 12	50.0	19.6 (13.2)	0.0206
<i>Melissodes comptoides</i>	CRP 12	37.4	27.1 (4.23)	0.0288
Forbs				
<i>Achillea millefolium</i>	PRA 12	48.7	28.0 (8.73)	0.0260
<i>Amorpha canescens</i>	PRA 12	94.5	29.9 (13.93)	0.0002
<i>Chamaecrista fasciculata</i>	CRP 12	100.0	26.5 (13.99)	0.0004
<i>Dalea candida</i>	PRA 12	81.5	31.8 (13.72)	0.0054
<i>Dalea purpurea</i>	PRA 12	67.0	29.7 (14.76)	0.0250
<i>Erigeron spp.</i>	CRP 14	81.0	60.3 (11.21)	0.0236
<i>Euphorbia corollata</i>	PRA 12	59.9	31.4 (14.49)	0.0266

APPENDIX N. continued...

<i>Hieracium longipilum</i>	PRA 12	53.3	24.4 (13.66)	0.0382
<i>Leucanthemum vulgare</i>	CRP 14	71.8	29.2 (11.76)	0.0016
<i>Linum sulcatum</i>	PRA 12	62.2	23.8 (11.94)	0.0214
<i>Mimosa microphylla</i>	PRA 14	54.3	27.4 (14.46)	0.0312
<i>Potentilla recta</i>	PRA 14	98.5	29.4 (13.66)	0.0002
<i>Psoraleidum tenuiflorum</i>	PRA 12	51.0	26.6 (10.95)	0.0444
<i>Rudbeckia hirta</i>	PRA 12	66.2	34.4 (8.54)	0.0006
<i>Salvia officinalis</i>	PRA 12	60.0	20.6 (12.63)	0.0282
<i>Symphotrichum ericoides</i>	PRA 12	75.1	27.2 (13.94)	0.0126
<i>Verbena stricta</i>	PAS 12	89.3	33.4 (14.26)	0.0014

Summary: This series of indicator species analyses reiterates what was described in Chapter 3. Most bee species with indicator status were collected from CRP sites in the 2012 season while most indicated forb species were in more abundant bloom in prairie sites in 2012. There are a few exceptions. *Augochlorella pura*, a small halictid bee, was counted in greater numbers from prairie sites in 2014, as were blooming *Potentilla recta*. The bumble bee *Bombus fervidus* was collected in greater numbers from pasture sites in 2014, which was not apparent without the seasonal analysis.

APPENDIX O. CORRELATIONS OF WOODLANDS AND POLLEN-BEARING BEES. Spearman rank and Pearson product moment correlations were performed to identify potential relationships between the percentage of woodlands surrounding a study site in the Southeast Prairies Biologically Unique Landscape, and the abundance of the most prominent pollen-bearing bee species. The correlation coefficient, ρ or r , is listed for each species, as well as p -values. Significance was determined after Holm-Sidak adjustments at $\alpha \leq 0.0125$, and significant correlations are indicated with boldface type. Species for which abundance data met the assumption of normal distribution in Shapiro-Wilk normality tests were assessed with Pearson product moment correlations, and are indicated in blue. All others are Spearman rank correlations.

Woodland Radius	All pollen-bearing bees	<i>Bombus pensylvanicus</i>	<i>Bombus auricomus</i>	<i>Eucera hamata</i>	<i>Agropostemon virescens</i>	<i>Xylocopa virginica</i>	<i>Megachile monticola</i>	<i>Bombus bimaculatus</i>	<i>Halictus parallelus</i>
250m ρ or r	0.163	0.063	-0.045	-0.217	0.261	-0.412	-0.334	-0.442	-0.453
p -value	0.562	0.823	0.875	0.437	0.348	0.127	0.223	0.099	0.090
400m	0.141	-0.057	-0.179	-0.342	0.084	-0.477	0.004	0.533	-0.324
	0.616	0.839	0.524	0.213	0.766	0.072	0.990	0.041	0.239
800m	0.305	-0.047	-0.177	-0.197	0.182	-0.293	-0.018	0.625	-0.255
	0.269	0.869	0.529	0.482	0.515	0.290	0.949	0.012	0.360
1200m	0.355	0.050	-0.211	-0.209	0.288	-0.026	-0.165	0.619	-0.140
	0.194	0.859	0.450	0.454	0.298	0.926	0.558	0.014	0.618